

THE ACCACOELIIDAE (DIGENEA) OF FISHES
FROM THE NORTH-EAST ATLANTIC

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SYNOPSIS

The family Accacoeliidae is considered to consist of two subfamilies, the Accacoeliinae and the Paraccacladiinae subfam. nov. The latter differs from the former in the configuration of the gut, the absence of a uroproct, the post-ovarian situation of Mehlis' gland and the structure of the vitellarium. Keys and original descriptions are presented for all of the accacoeliids so far recorded from the north-east Atlantic region together with full host-records, locality-data and comments on some aspects of their biology. The species described are: *Accacoelium contortum*, *Accacladium serpentulum*, *Accacladocoelium nigroflavum*, *A. alveolatum*, *A. macrocotyle*, *A. petasiporum*, *Rhynchopharynx paradoxa* and *Odhnerium calyptrocotyle*, all from *Mola mola*; *Tetrochetus raynerii* from *Luvarus imperialis*; *Paraccacladium jamiesoni* gen. et sp. nov. from *Coryphaenoides rupestris* and *P.* sp. (immature) from alepocephalid and centrolophid fishes.

INTRODUCTION

THE HELMINTHS of marine fishes from the north-east Atlantic region have been studied for about 200 years by numerous workers, notably Olsson, van Beneden, Odhner, Nicoll, Lebour, Dollfus, Baylis, Punt, Sproston, Rees, Brinkmann, Williams and Berland. Except, however, for the works of Nicoll (1915), Dawes (1947) and Dollfus (1953) little has been done to compile lists or detailed descriptions of these parasites into comprehensive works. Our aim is to produce complete descriptions,

figures and keys based, wherever possible, on original material, as we feel that this is much more satisfactory than depending entirely upon existing descriptions which are often inadequate. This is the first of a projected series of papers covering all groups of parasitic helminths. The region covered by this series is enclosed by a line drawn from Gibraltar to Cape Farewell in Greenland. It includes the North Sea, Skagerrak, Kattegat, Irish Sea and English Channel, but not the Baltic or the Barents Seas.

MATERIALS AND METHODS

Wherever possible original material has been studied. Some of this material has been deposited in the British Museum (Natural History) over the years, and its method of preservation is often unknown and varies considerably. The material collected by ourselves was obtained during two visits to Plymouth in 1972 (by D. I. G.), four trips to the North Atlantic aboard the R.V. *Cirolana* in 1971, 1973, 1974 and 1975 (by R. A. B.) and one visit to Aberdeen in 1973 (by both authors). The fish from Plymouth and Aberdeen were obtained from catches made by vessels of the Marine Biological Association and commercial fishing vessels, respectively. All fish were dissected shortly after capture, usually being freshly killed. The worms, except cestodes, were fixed in glacial acetic acid for about 1 minute and preserved in 80% alcohol. Cestodes were fixed using formol-acetic-alcohol, 4% formalin or hot alcohol, usually under pressure. Whole-mounts were stained in Mayer's paracarmine and mounted in Canada balsam. Wherever possible, examples of the platyhelminth species were sectioned and stained with Mayer's haemalum and eosin (H. and E.). Our studies indicate that, whereas it is usually essential to section platyhelminth-material for the purpose of accurate determination, it is imperative for their description.

The descriptions, in which certain key words are italicized, are, where possible, original, and the references of previous recognizable descriptions are given prior to our own.

SYSTEMATIC SECTION

The classification of the family Accacoeliidae is a matter of some contention. Three main proposals have been put forward: (1) Dollfus (1935, 1960a) accepts two subfamilies, the Accacoeliinae and the Tetrochetinae; (2) Skrjabin & Guschanskaja (1959) accept five subfamilies, the Accacoeliinae, Guschanskianinae, Orophocotylinae, Rhynchopharynginae and Tetrochetinae; and (3) Yamaguti (1958) accepts four, the Accacoeliinae, Accacladiinae, Orophocotylinae and Rhynchopharynginae, and later (1971) five subfamilies, including the Guschanskianinae. Dollfus (1960a) indicates that the systems presented by Yamaguti and by Skrjabin & Guschanskaja are, in neither case, satisfactory. Dollfus' detailed criticism has, however, produced no reaction from Yamaguti (1971). We believe that Dollfus' classification is by far the most acceptable of the three, but prefer to place all of the genera known hitherto into one subfamily, the Accacoeliinae, as the two subfamilies accepted by Dollfus clearly grade into one another in the form of *Odhnerium* Yamaguti, 1934. This will be discussed in more detail elsewhere (p. 86). We do, however, consider it necessary to erect a second subfamily, the Paracccladiinae, for *Paracccladium*, a new genus

to be described in this paper. It differs from the remainder of the accacoeliids in the structure of the gut, the vitellarium and in the post-ovarian position of Mehlis' gland. The latter subfamily appears to have a morphology somewhat intermediate between the accacoeliine accacoeliids and the sclerodistomids. Full details of classification and definitions of these taxa will be presented elsewhere (Gibson & Bray, in prep.).

The classification of the accacoeliids is based primarily on the structure of the reproductive system. Although most of the terminology relating to the reproductive system is well established, there are two features of the terminal genitalia which are less familiar, as they tend to be restricted to hemiurioids. The sinus-organ is an intromittent copulatory process lying within the genital atrium and through which runs the hermaphroditic duct. The sinus-sac (hermaphroditic-sac) is a muscular structure which surrounds the base of the genital atrium, and into which both male and female ducts pass. This structure appears to be partly analogous with the cirrus-sac of many other digeneans in that it usually contains an intromittent organ. These two features can only be studied satisfactorily in serial sections.

Aspects of Biology

Adults of all but two of the ten species of accacoeliids from the north-east Atlantic are recorded from the sun-fish *Mola mola*. One of the other species, which we believe represents a new subfamily, is recorded from the macrourid *Coryphaenoides rupestris*. Further immature forms of the same genus are described from alepocephalid and centrolophid fishes. The parasites of *Mola mola* represented in the region are all widespread, and are probably present wherever their wide-ranging host is found. *Mola mola* is described as a 'high-ocean circum-global warm-water fish' by Ekman (1953).

The first intermediate host of accacoeliids is not known, but numerous records indicate that the metacercariae are found in planktonic animals. *Metacercaria owreae* Hutton, 1954, was thought by Dawes (1959) to be the cercaria of a species of *Accacladocoelium* Odhner, 1928. This larva has been recorded in both Atlantic and Indian Oceans from many species of planktonic chaetognaths. The evidence that this larva is in fact an accacoeliid is not unequivocal although the configuration of the gut is somewhat like that of the accacoeliines. More certain identifications of accacoeliid metacercariae have been made on specimens from siphonophores, scyphomedusae, ctenophores and chaetognaths. These records are summarized by Dollfus (1963) and Rebecq (1965). In fact, the original description of *Odhnerium calyptrocotyle* (Monticelli, 1893) is based on specimens from the ctenophore *Beroe ovata*. Nikolaeva (1968) has recorded various immature accacoeliids from pelagic fishes in the Mediterranean Sea, and considers that these represent 'cystless' metacercariae. The pelagic teleosts may, therefore, act as paratenic hosts. Presumably this is how such predatory fishes as *Coryphaena* and *Coryphaenoides*, the usual final hosts of *Tetrochetus coryphaenae* Yamaguti, 1934, and *Paraccacladium*, respectively, become infested. It is worthy of note that, according to Bigelow & Schroeder (1953), *Mola mola*, as a rule, feeds upon coelenterates, ctenophores and salps, and that all four species of teleost from which we have recorded immature specimens of

Paraccacladium sp. are known to feed extensively on medusae. Furthermore, the stomach of one of the latter teleosts, *Alepocephalus bairdii*, was found by us to be filled with the bathypelagic scyphomedusa *Atolla wyvillei*. *Luvarus imperialis*, the host of *Tetrochetus raynerii*, also 'feeds primarily upon jellyfish and similar gelatinous planktonic forms' (Fitch & Lavenberg, 1971). Other species of *Tetrochetus* and *Paraccacladium jamiesoni* have been recorded as adults in predatory fishes, and, therefore, it seems likely that the suggested paratenic teleost-host may, in fact, be an obligatory intermediate host. Within the Accacoeliidae it is possible, therefore, that there are two types of life-history: (1) direct from the coelenterate, etc., when sun-fishes and *Luvarus* are the final hosts; and (2) via a coelenterate-feeding teleost (?) third intermediate host when predatory teleosts are the final hosts.

Family ACCACOELIIDAE Odhner, 1911

DIAGNOSTIC FEATURES. Body large or small, commonly elongate. Body-surface smooth, but forebody may be papillate. Ventral sucker in anterior half of body, may be pedunculate. Prepharynx absent. Pharynx well developed, with narrow extension into base of oral sucker. Gut-caeca with or without long, anteriorly directed diverticula; terminate blindly or form uroproct. Testes two, usually oblique but may be symmetrical or in tandem, normally close to middle of body; pre-ovarian. Seminal vesicle thin walled, tubular, sinuous or convoluted, commonly reaching into hindbody. Pars prostatica tubular. Hermaphroditic duct, sinus-sac and sinus-organ usually present. Genital pore mid-ventral in anterior region of forebody. Genital atrium present. Ovary oval; post-testicular Laurer's canal and uterine seminal receptacle present. Uterus extensive, usually reaching to posterior extremity before looping forward. Eggs small, very numerous, non-filamented. Vitellarium composed of numerous filamentous tubules; with or without left side of system reduced to a rudiment. Excretory vesicle Y-shaped; arms initially in dorsal and ventral fields, unite dorsally to pharynx or oral sucker.

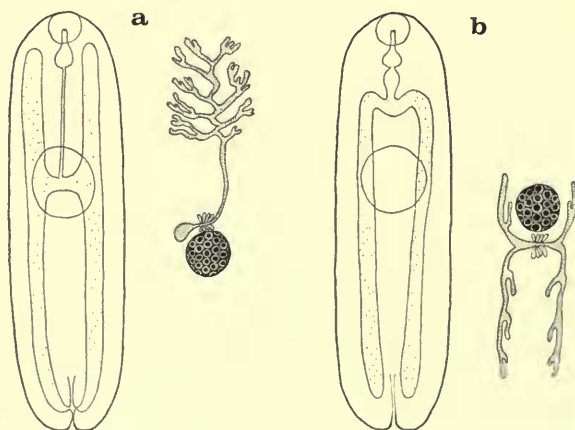


FIG. 1. Diagrams of intestinal and vitelline configuration in (a) Accacoeliinae and (b) Paraccacladiinae.

KEY TO THE SUBFAMILIES OF THE ACCACOELIIDAE IN
THE NORTH-EAST ATLANTIC REGION

1. A. Gut distinctly H-shaped ; uroproct present ; oesophagus very long and narrow ; vitellarium with single main collecting duct and system of branching tubules ; Mehli's gland pre-ovarian *Accacoeliinae* (Fig. 1a) (p. 57)
- B. Gut not clearly H-shaped ; uroproct absent ; oesophagus relatively short and stout ; vitellarium with symmetrical pair of collecting ducts and systems of branching tubules ; Mehli's gland post-ovarian *Paraccaceliinae* (Fig. 1b) (p. 90)

Subfamily **ACCACOELIINAE** Odhner, 1911

Tetrochetinae Looss, 1912, emend. Dollfus, 1935.

Accaceliinae Yamaguti, 1958.

Orophocotylinae Yamaguti, 1958.

Rhynchopharynginae Yamaguti, 1958.

Guschanskianinae Skrjabin, 1959.

DIAGNOSTIC FEATURES. Body usually elongate. Oesophagus long and narrow. Gut H-shaped. Uroproct present. Mehli's gland pre-ovarian. Vitellarium filamentous, with single main collecting duct and single system of ramifying branches in fore- or hindbody ; left side of system reduced.

KEY TO THE GENERA OF THE ACCACOELIINAE IN
THE NORTH-EAST ATLANTIC REGION

1. A. Well-defined sinus-sac and sinus-organ absent 2
- B. Well-defined sinus-organ and sinus-sac present (*i.e.* clearly visible in sections) 3
2. A. No sinus-organ, but small male papilla may be present ; sinus-sac rudimentary ; sucker-like muscular pads present dorsally in forebody ; two muscular flanges on ventral sucker *Odhnerium* Yamaguti, 1934 (p. 81)
- B. Sinus-organ and sinus-sac absent ; antero-dorsal muscular pads and flanges on ventral sucker absent *Tetrochetus* Looss, 1912 (p. 86)
3. A. Ectoparasitic on gills ; strongly developed ventral musculature in hindbody ; very long proboscis-like sinus-organ ; enormous pars prostatica occupying much of forebody ; vitellarium posterior to anterior testis *Accacoelium* Monticelli, 1893 (p. 57)
- B. Endoparasitic in gut ; short, cylindrical or dome-shaped sinus-organ ; vitellarium not usually extending posteriorly to ovary 4
4. A. Pharynx pyriform with anterior extension into base of oral sucker 5
- B. Pharynx consists of two bulbs and an anterior, elongate portion ensheathed in glandular posterior process of oral sucker ; glandular oesophageal bulb immediately posterior to pharynx ; large glandular structure of unknown function at base of peduncle of ventral sucker *Rhynchopharynx* Odhner, 1928 (p. 77)
5. A. Vitellarium confined to hindbody ; ventral sucker on extensible peduncle ; pars prostatica relatively short *Accacelium* Odhner, 1928 (p. 61)
- B. Vitellarium wholly or partly in forebody ; ventral sucker sessile or nearly so ; pars prostatica relatively long *Accaceladocoelium* Odhner, 1928 (p. 65)

ACCACOELIUM Monticelli, 1893

DIAGNOSTIC FEATURES. Forebody papillate. Oesophagus reaches to ventral sucker. Ventral sucker on short peduncle. Thick muscular layer in ventral hindbody. Sinus-sac present, surrounding base of genital atrium. Sinus-organ long

and strongly muscular, frequently extending through genital pore. Enormous pars prostatica and associated gland-cells occupy much of forebody. Vitellarium posterior to anterior testis. Parasitic on gills of marine teleosts (*Mola*).

TYPE-SPECIES. *Accacoelium contortum* (Rudolphi, 1819) (by subsequent designation : Looss, 1899, 631).

***Accacoelium contortum* (Rudolphi, 1819) Looss, 1899**

(Figs 2 and 3)

Distoma contortum Rudolphi, 1819.

Podocotyle contortum (Rud.) Stossich, 1898.

TYPE-HOST AND LOCALITY. *Mola mola*, Naples, Italy.

RECORDS.

(i) Material studied.

Mola mola [gills] Skagen, Denmark (58°N, 11°E) (Oct. 1923). Natural History Museum of Gothenburg Reg. No. 23-3991.

Mola mola [gills] Locality unknown. BM(NH) Reg. No. 1973.1.25.17-20.

(ii) From the literature.

Mola mola [gills] Ireland (July 1839). Bellingham (1844 : 427).

Mola mola [gills] Varberg, Sweden (Nov.). Olsson (1868 : 39).

PREVIOUS DESCRIPTIONS. Olsson (1868) ; Monticelli (1893) ; Linton (1898, 1940) ; Timon-David & Musso (1971).

DESCRIPTION. Fig. 2 represents the shape assumed by all the specimens, although in some cases the hindbody is longer in proportion to the forebody. The body-surface is not spined, but very wrinkled due to contraction, and numerous papillae ornament the forebody. The *ventral sucker* is borne on a short peduncle. Ventrally in the parenchyma of the hindbody there is a thick layer of longitudinal muscle.

The measurements given in Table 1 are taken from laterally mounted specimens. Anteriorly, the *pharynx* extends into the base of the *oral sucker* forming a conical projection (Fig. 3), the main body of the pharynx measuring 0.3 mm in diameter. There is a long, narrow oesophagus, which measures about 2 mm and possesses a cuticular lining. It bifurcates dorsally to the ventral sucker to form two caeca which give off anteriorly-directed blind extensions. The wide, laterally undulating caeca reach close to the posterior extremity, where they unite with the excretory vesicle to form a uroproct.

The terminal *excretory pore* leads into an excretory vesicle which is essentially Y-shaped, the basal region being very short. Closely anterior to the union with the gut-caeca, the vesicle divides forming a dorsal and a ventral arm, which are convoluted and pass anteriorly. They run laterally in the forebody and unite behind the pharynx.

The *testes* are irregularly globular or oval, situated in tandem and quite close together in the anterior half of the hindbody. The seminal vesicle is a relatively narrow and greatly convoluted tube, lying mainly dorsally to the ventral sucker. At about the level of the anterior margin of this sucker the seminal vesicle narrows and

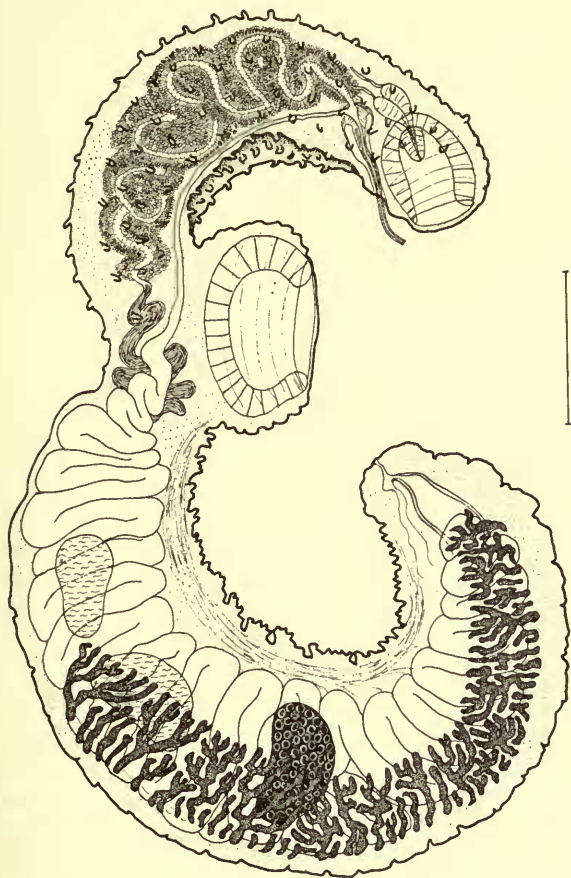


FIG. 2. *Accacoelium contortum*: lateral view (gut omitted). Scale = 1 mm.

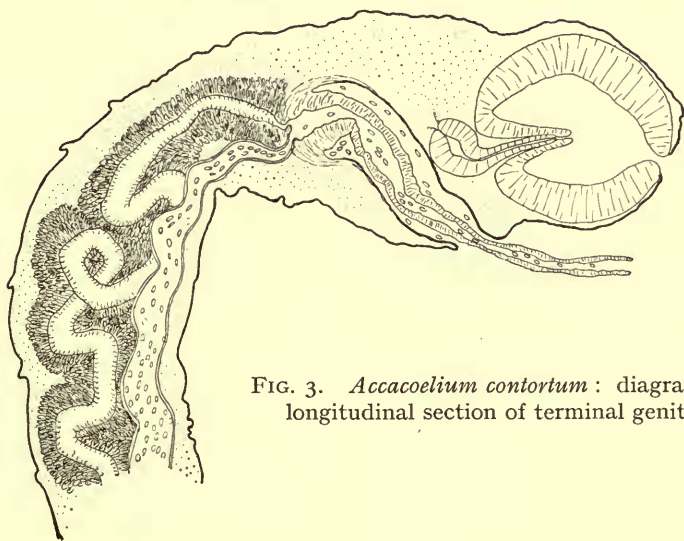


FIG. 3. *Accacoelium contortum*: diagrammatic longitudinal section of terminal genitalia.

TABLE I

The dimensions of *Accacoeilium contortum* from *Mola mola* as recorded by various authors

Locality	Olsson, 1868	Monticelli, 1893	Linton, 1898	Linton, 1940	Timon-David & Musso, 1971	Present Study
	Sweden	?	?	Massachusetts, USA	Gulf of Marseilles	see text
Length, mm	17	15-25	8	10-15	16-18.5	5-17
Max. width, mm	3	-	0.72	1-2	1.3-2	1.3-2
Oral sucker, mm	-	-	0.6 long	0.5-0.7 x	0.71-1.0 x	0.38-0.70 x
Ventral sucker, mm	-	-	0.7 long	0.38-0.91	0.56-0.95	0.62-0.89
Pharynx, mm	-	-	-	0.63-1.12 x	0.87-1.36 x	0.86-1.0 x
Testes, mm	-	-	-	0.56-1.4	1.0-1.5	0.97-1.14
Ovary, mm	-	-	-	0.28-0.42 x	0.28-0.33 x	0.23-0.3 x
Eggs, μ m	-	-	-	0.14-0.21	0.21-0.4	0.29-0.35
				-	1.47-1.93 x	0.51-1.08 x
				-	1.2-1.72	0.9-1.3
				-	0.91-1.0 x	0.48-0.9 x
				-	0.82-0.95	0.48-0.54
			30-36 x 20	maximum	27-30 x	27-34 x
			33 x 21	33 x 21	16-20	19-22

leads into an enormous, convoluted and tubular pars prostatica, which occupies much of the forebody of the worm. The duct is surrounded by a deep layer of large glandular cells which are delimited by either a membrane or a local compaction of parenchyma. A very short ejaculatory duct leads from the pars prostatica, through the wall of the *sinus-sac*, into the base of the hermaphroditic duct. The latter is long, running as it does through the centre of a long, muscular sinus-organ (Fig. 3). The sinus-organ is frequently found extended through the genital pore, which occurs mid-ventrally close behind the oral sucker. When withdrawn, the sinus-organ does not appear to contract as much as is seen in some other hemiuroids, but lies folded within the deep genital atrium. The sinus-sac envelops the proximal extremity of the genital atrium, and consists of a relatively diffuse musculature.

The *ovary* is transversely oval and of a similar size to the testes. It is post-testicular, lying just inside the posterior half of the hindbody. The oviduct, on leaving the ovary, passes into a compact, but well-developed, Mehlis' gland which lies directly anterior to the ovary. Before entering Mehlis' gland, however, it receives the common vitelline duct and Laurer's canal. The latter passes antero-dorsally and opens to the exterior dorsally to the posterior testis. The first coils of the *uterus* contain large amounts of sperm, and thus form a uterine seminal receptacle which lies between the ovary and the posterior testis. The remainder of the uterus fills much of the hindbody, is greatly convoluted and contains numerous small operculate eggs. The uterus becomes much less convoluted as it passes dorsally to the ventral sucker, and then runs forward, undulating gently, to its union with the ejaculatory duct at the base of the sinus-sac. This latter part of the uterus within the forebody, which may be referred to as the metraterm, is lined by a narrow epithelial layer, possesses a muscular wall and is invested by a thin layer of glandular cells. The *vitellarium* consists of a complicated ramifying system of tubules, lying laterally between the level of the anterior testis and the posterior end of the body. This system is drained by a single (right) main collecting duct, the left-hand system being reduced to a small blind 'vitelline reservoir' which lies ventrally to Mehlis' gland.

DISCUSSION. This is the only known species of the genus and is unusual because of its ectoparasitic habitat on the gills. Morphologically it is rather similar to *Accacladium*, which normally occurs in the intestine of *Mola mola*. It is possible that the well-developed ventral musculature of the hindbody is associated with a prehensile function, as the animal must be continually exposed to the stream of water over the gills.

ACCACLADIUM Odhner, 1928

DIAGNOSTIC FEATURES. Body-surface smooth. Oesophagus reaches to ventral sucker. Ventral sucker on short peduncle. Pars prostatica fairly well developed. Sinus-sac surrounding base of genital atrium. Sinus-organ short, cylindrical. Vitellarium between ventral sucker and ovary. Parasitic in intestine of marine teleosts (*Mola*).

TYPE-SPECIES. *Accacladium serpentulum* Odhner, 1928 (by original designation and monotypy).

Accacladium serpentulum Odhner, 1928

(Fig. 4)

Distomum nigroflavum of Monticelli, 1893, and of Linton, 1898, *nec* Rudolphi, 1819.*Accacladium nematulum* Noble & Noble, 1937.TYPE-HOST AND LOCALITY. *Mola mola*, Bergen, Norway.

RECORDS.

(i) Material studied.

Mola mola [intestine] Kattegat, Sweden (58°N, 11°E) (Dec. 1929). Natural History Museum of Gothenburg Reg. No. 29-5153.

(ii) From the literature.

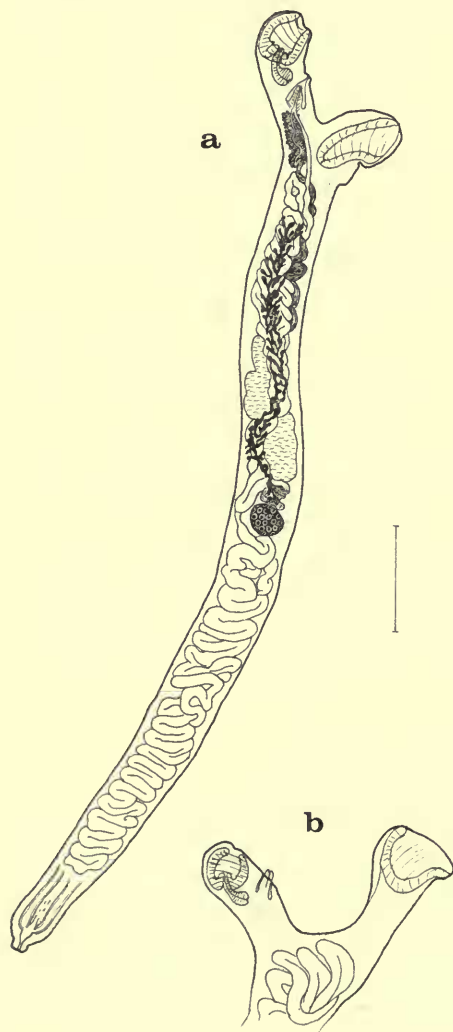
Mola mola [intestine] Bergen, Norway. Odhner (1928 : 173).

FIG. 4. *Accacladium serpentulum*: (a) lateral view (gut omitted); (b) forebody showing peduncle extended. Scale - 2 mm.

PREVIOUS DESCRIPTIONS. Monticelli (1893); Odhner (1928); Linton (1898, 1940); Yamaguti (1934); Noble & Noble (1937); Timon-David & Musso (1971).

DESCRIPTION. Two whole worms were available for study, the dimensions of which are given in Table 2.

The body of this form is elongate, with the *ventral sucker* surmounted upon a peduncle of variable length (Fig. 4a and b). The body-surface is smooth, lacking papillae. The *oral sucker* is globular with a prominent conical projection at its base, caused by the elongate anterior portion of the *pharynx*. A long, narrow, oesophagus leads from the pharynx and reaches back at least to the level of the ventral sucker. The H-shaped gut-caeca reach forward, from the region of the ventral sucker, to the pharyngeal region and backward to the posterior extremity, where they connect with the excretory vesicle to form a uroproct.

The *excretory vesicle* is Y-shaped, the arms being dorsal and ventral in the hindbody, lateral in the forebody, and uniting dorsally in the region of the pharynx. The basal region of the vesicle is very short.

The elongate oval *testes* may have slightly indented margins and occur in the middle-region of the hindbody, with the posterior testis lying ventrally and the anterior testis dorsally. The seminal vesicle is long, tubular, coiled and reaches from just in front of the anterior testis to a region dorsal to the ventral sucker. The pars prostatica is also coiled and is surrounded by numerous gland-cells. It passes anteriorly from the level of the ventral sucker to the base of the *sinus-sac*. A very short ejaculatory duct joins with the metraterm just inside the sinus-sac to form the hermaphroditic duct, which runs through a prominent, muscular sinus-organ. The latter organ is not as large as that in *Accacoelium*, but may protrude through the genital pore, and lies in a fairly deep genital atrium. The genital pore is mid-ventral in the forebody, slightly posterior to the oral sucker. The sinus-sac, which surrounds the base of the genital atrium, is composed of diffuse muscle and is somewhat difficult to distinguish in whole-mounts.

The post-testicular *ovary* is more or less globular, and Mehlis' gland is pre-ovarian. Laurer's canal has been described by other authors, and a uterine seminal receptacle is present. The *uterus* itself reaches fairly close to the posterior extremity and fills much of the hindbody. The metraterm may be distinguished by its thick wall. The *vitellarium* consists of numerous branching tubules which extend from just posterior to the peduncle of the ventral sucker to the anterior margin of the ovary.

DISCUSSION. Odhner's (1928) is the only previous record of this species from the north-east Atlantic, but it has been recorded in the Mediterranean Sea as well as on the Atlantic and Pacific coasts of North America and off Japan. Noble & Noble (1937) described a new species, *A. nematulum*, from off California, but its validity does seem somewhat questionable. Very similar specimens under the same name have been described from the Mediterranean Sea by Timon-David & Musso (1971), and this description suggests that the Californian form may not be distinct. Noble & Noble comment on five characters which they consider may separate *nematulum* and *serpentulum*. As far as the length, length-width ratio and elongation of hindbody is concerned, there is little doubt that this species is variable enough to invalidate these distinctions (see Table 2). The size and shape of the ventral sucker

TABLE 2

The dimensions of *Accacliadium serpentulum* from *Mola mola* as recorded by various authors

Name used	Monticelli, 1893	Linton, 1898	Odhner, 1928	Yamaguti, 1934	Noble & Noble, 1937	Linton, 1940	Timon-David & Musso, 1971	Present Study
Locality	<i>Distomum nigroflavum</i> ?	Mass., USA	Norway	Japan	California, USA	Mass., USA	Gulf of Marseilles	Sweden
Length, mm	8-23	up to 35	20-30	22.2	8.22-17.6	4-12	2.38-24	19-22
Max. width, mm	-	1.12	0.9-1.25	1.2	0.46-0.83	1.12	0.55-1.5	1.2-1.5
Forebody, mm	-	-	2.4-3.3	-	0.96-2.37	2.38	0.9-3.1	2.1-2.2
Oral sucker, mm	-	-	0.7-0.83	0.75 x 0.78	0.46-1.02 x 0.36-0.66	0.7 x 0.63	0.42-1.05 x 0.39-1.1	0.86 x 0.86-1.02
Ventral sucker, mm	-	-	1.0-1.2 x 0.7 deep	-	0.31-0.6 x 0.53-1.59	0.91 x 0.63	0.37-0.89 x 0.79-1.46	0.65-1.08 x 1.4-1.68
Pharynx, mm	-	-	-	0.23 x 0.23	0.2-0.29 x 0.13-0.17	0.35 x 0.14	0.13-0.3 x 0.09-0.3	0.22-0.34 x 0.58-0.6
Testes, mm	-	1.12-1.03	-	1.25 x 0.75-0.8	0.63-1.37 x 0.32-0.64	-	0.22-1.9 x 0.22-1.3	0.65-0.7 x 1.35-1.65
Ovary, mm	-	-	-	-	0.22-0.81 x 0.15-0.55	-	0.05-1.22 x 0.05-1.00	0.65-0.69 x 0.7-1.22
Eggs, μ m	-	30 x 20	28-29 x 17-20	36 x 22	31-37 x 21-23	27-30 x 19-21	27-30 x 15-20	30-36 x 22-27

probably vary with fixation, and the egg-size, as recorded by various authors, has a continuous range of $27-37\ \mu\text{m} \times 17-27\ \mu\text{m}$. Finally, the size of the sinus-organ should not be considered as a taxonomic criterion, as it is a protrusible muscular organ and can therefore be expected to be found in a number of conditions, and indeed may be influenced by fixation techniques. We, therefore, consider these species to be identical.

ACCACLADOCOELIUM Odhner, 1928

Guschanskiana Skrjabin, 1959.

DIAGNOSTIC FEATURES. Body smooth. Lateral flanges on ventral sucker occasionally present. Oesophagus reaches to ventral sucker. Pars prostatica long. Sinus-sac surrounding base of genital atrium. Sinus-organ short, cylindrical. Vitellarium reaches anteriorly to oral sucker, may extend posteriorly just past ovary but usually not beyond anterior testis. Parasitic in intestine of marine teleosts (*Mola*).

TYPE-SPECIES. *Accacladocoelium nigroflavum* (Rudolphi, 1819) (by original designation).

KEY TO SPECIES IN NORTH-EAST ATLANTIC REGION

1. A. Muscular flanges on ventral sucker absent 2
 B. Muscular flanges on ventral sucker present *A. petasiporum* Odhner, 1928 (p. 75)
2. A. Vitellarium reaching to anterior margin of anterior testis 3
 B. Vitellarium reaching just posterior to ovary *A. macrocotyle* (Diesing, 1858) (p. 72)
3. A. Numerous small papilla-like extensions at posterior end
 *A. alveolatum* Robinson, 1934 (p. 68)
 B. Normal body-surface at posterior end *A. nigroflavum* (Rudolphi, 1819) (p. 65)

Accacladocoelium nigroflavum (Rudolphi, 1819) Robinson, 1934 (Fig. 5)

Distoma nigroflavum Rudolphi, 1819.

Accacoelium nigroflavum (Rud.) Lühe, 1901.

Echinostoma nigroflavum (Rud.) Barbagallo & Drago, 1903.

Distoma megnini Poirier, 1885.

Accacladocoelium megnini (Poirier) Dollfus, 1946.

TYPE-HOST AND LOCALITY. *Mola mola*, Naples, Italy.

RECORDS.

(i) Material studied.

Mola mola [intestine] Kattegat, Sweden (58°N , 11°E) (Dec. 1929). Natural History Museum of Gothenburg Reg. No. 29-5153.

Mola mola [intestine] Rockall, N Atlantic (Aug. 1956). BM(NH) Reg. No. 1964.7.16.1-20.

Mola mola [intestine] Porlock, Somerset, England (Aug. 1966). BM(NH) Reg. No. 1967.10.2.1-10.

(ii) From the literature.

Mola mola [intestine] Ireland (July 1839). Bellingham (1844 : 427).

Mola mola [intestine] Atlantic WSW of Great Britain (48°N 19°W) (Sept. 1886).

Guiart (1938 : 41).

PREVIOUS DESCRIPTIONS. Poirier (1885) ; Timon-David & Musso (1971).

LIFE-HISTORY. Not known, but Dawes (1959) claims that *Metacercaria owreae* Hutton, 1954, is the cercaria of a species of *Accacladocoelium* (see above p. 55). This larval form was recorded from chaetognaths, but it seems likely that *Accacladocoelium* spp., like other accacoeliine genera, also use coelenterates and ctenophores as intermediate hosts.

DESCRIPTION. This description is based on six whole-mounts and one sectioned specimen. The worms have an elongate, roughly cylindrical shape, with a prominent *ventral sucker* situated close to the anterior end (Fig. 5). Maximum breadth is at the level of the ventral sucker. The dimensions of this worm are given in Table 3. The body-surface is irregularly rugate, but bears no spines, papillae or regular plications.

TABLE 3

Dimensions of *Accacladocoelium nigroflavum* as recorded by various authors

	Poirier, 1885	Timon-David & Musso, 1971	Present Study
Name used	<i>Distoma megnini</i>	<i>Accacladocoelium nigroflavum</i>	<i>Accacladocoelium nigroflavum</i>
Host	unknown fish	<i>Mola mola</i>	<i>Mola mola</i>
Locality	?	Gulf of Marseilles	see text
Length, mm	10	8.9-10.7	6.5-25
Max. width, mm	0.3	1.5-1.55	1.04-1.86
Oral sucker, mm	-	0.40-0.42 × 0.48-0.50	0.31-0.86 × 0.43-0.97
Ventral sucker, mm	2.0	0.81-1.04 × 0.74-0.84	0.86-1.0 × 0.97-1.62
Pharynx, mm	-	0.19-0.20 × 0.15	0.31 × 0.54
Testes, mm	-	1.03-1.15 × 0.76-1.02	0.50-2.16 × 0.30-0.86
Ovary, mm	-	0.82-0.91 × 0.72-0.78	0.22-0.68 × 0.43-0.89
Eggs, µm	28 × 21	25 × 15	24-36 × 16-25

An anterior extension of the *pharynx* protrudes into the base of the *oral sucker*. A very narrow (0.025 mm) and long (about 2 mm) oesophagus reaches back to about the posterior margin of the ventral sucker, where it leads into wide gut-caeca which have anterior extensions reaching to the level of the pharynx. The caeca reach nearly to the posterior end of the body where they open into the excretory vesicle, forming a uroproct.

The terminal *excretory pore* leads into a Y-shaped excretory vesicle, the arms of which pass dorsally and ventrally in the hindbody, but could not be traced in the forebody.

The large oval *testes* lie in tandem, near the ventral surface, or with the anterior testis more dorsal than the posterior, and fairly close behind the ventral sucker. The seminal vesicle is a relatively narrow, convoluted tube, lying dorsally to the

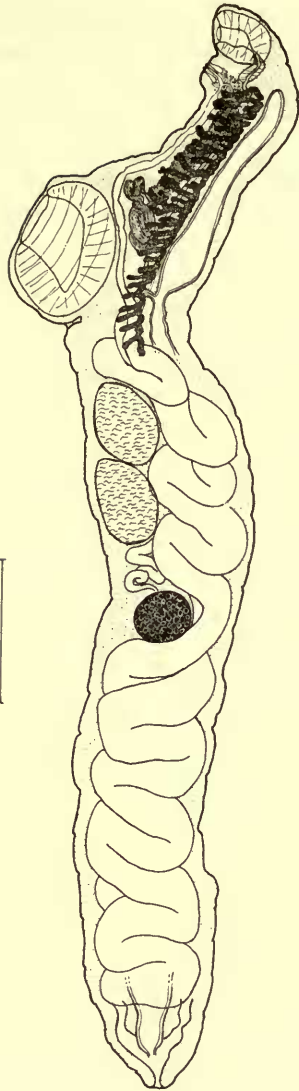


FIG. 5. *Accacladocoelium nigroflavum*: lateral view (most of gut omitted). Scale - 1 mm.

ventral sucker. At about the level of the anterior margin of the ventral sucker, the seminal vesicle passes, via a short, aglandular duct, into a long gently sinuous pars prostatica which reaches to the base of the sinus-sac. The pars prostatica is surrounded by numerous gland-cells lying free in the parenchyma. The *sinus-sac* is a small, rather weakly-developed muscular structure surrounding the base of the genital atrium. Just within the wall of the sac a very short ejaculatory duct unites with the metraterm to form a hermaphroditic duct, which passes through the centre of a small, cylindrical sinus-organ. The latter usually almost fills the genital atrium and may extend slightly through the genital pore, which is situated ventrally to the pharynx.

The globular *ovary* is situated posteriorly to the testes in the middle of the body. Immediately anterior to the ovary lies a large Mehlis' gland. Laurer's canal leaves the oviduct, passes close to the level of the posterior margin of the ovary before running across the body and opening dorsally at the level of the anterior margin of the ovary. The initial coils of the *uterus* contain much spermatozoa, forming a fairly compact uterine seminal receptacle. The remainder of the uterus, containing numerous eggs, fills the bulk of the hindbody, and passes well forward into the forebody with one loop reaching almost to the pharynx. The metraterm reaches from the posterior margin of the ventral sucker to just inside the sinus-sac and is surrounded by gland-cells. The *vitellarium* consists of a ramifying system of tubules which, while mostly confined to the forebody of the worm, may reach to the anterior testis. Ventrally to the ovary lies a large 'vitelline reservoir', which communicates with Mehlis' gland by means of a short duct. This 'reservoir' and duct is, apparently, all that remains of the left side of the vitelline system.

DISCUSSION. Poirier (1885) describes and figures this species very well under the name *Distoma megnini*. Odhner (1928), after examining about sixty of Rudolphi's original specimens of *Distomum nigroflavum*, considered them to be synonymous with Poirier's form. The specimen of *D. nigroflavum* figured by Olsson (1868) lacks a sinus-organ and apparently has the sucker-like pads on the antero-dorsal surface which are so characteristic of *Odhnerium calyptrocotyle*. The record of this latter species from Varberg by Dollfus (1935) suggests that he considered that Olsson's specimens belong to *O. calyptrocotyle*. We agree with this and have, therefore, included *D. nigroflavum* of Olsson as a synonym of *O. calyptrocotyle*.

***Accacladocoelium alveolatum* Robinson, 1934**

(Fig. 6)

Guschanskiana alveolatum (Robinson) Skrjabin, 1959.

TYPE-HOST AND LOCALITY. *Mola mola*, Devon, England.

RECORDS.

(i) Material studied.

Mola mola [intestine] Salcombe, Devon, England. BM(NH) Reg. No. 1968.12.2.103-104. [Two type-specimens which were originally deposited in the Molteno Institute, Cambridge, and were presented to the British Museum (Natural History) in 1968.]

Mola mola [intestine] Kattegat at Gothenburg, Sweden. Material lent by J. Thulin.

Mola mola [intestine] Whitby, Yorkshire, England (Aug. 1973). BM(NH) Reg. No. 1975.10.31.25.

(ii) From the literature.

Mola mola [intestine] Salcombe, Devon, England (June, 1933). Robinson (1934 : 346).

Mola mola [intestine] Kattegat at Gothenburg, Sweden (Nov. 1971). Thulin (1973 : 83).



FIG. 6. *Accacladocoelium alveolatum*: lateral view (most of gut omitted). Scale - 1 mm.

PREVIOUS DESCRIPTIONS. Robinson (1934); Thulin (1973).

DESCRIPTION. Based upon two type-specimens, one of which we sectioned, four flattened specimens from Yorkshire and on two flattened and one sectioned specimen from Thulin. The original specimens are contracted and the tegument is thrown into numerous annular rugae, which are much less evident in Thulin's material. As pointed out by Robinson (1934), the peculiar distribution of minute papillae at the posterior end of the body gives the superficial appearance of a large terminal sucker (Fig. 6). The *oral sucker* and sessile *ventral sucker* were measured from sections in lateral view. The various dimensions of these worms are included in Table 4.

The *pharynx* is relatively small and extends forward slightly into the base of the oral sucker. A long, narrow, oesophagus passes back to the level of the posterior margin of the ventral sucker, where it divides to form two somewhat convoluted gut-caeca, which extend forward to the level of the pharynx and backward close to the posterior extremity, where they join with the excretory vesicle to form a uroproct.

TABLE 4
Dimensions of *Accacladocoelium alveolatum* from *Mola mola* as recorded by various authors

Locality	Robinson, 1934	Robinson's types	Thulin, 1973	Thulin's specimens	Present Study
Length, mm	Devon, England	Devon, England	Kattegat, Sweden	Kattegat, Sweden	Yorkshire, England
Max. width, mm	6.5	6.0	14 (largest)	11-14 (flattened)	7.5-10 (flattened)
Oral sucker, mm	1.5	2.0	1.7 (largest)	1.8-2.5	1.8-2.1
	0.5	0.5 x 0.56	-	0.51-0.52 x 0.55	0.36-0.39 x
Ventral sucker, mm	1.0	1.04 x 0.92	-	1.35-1.38 x	0.43-0.56
Pharynx, mm	poorly developed	0.2 x 0.08	-	1.22-1.27	1.22-1.49 x
Testes, mm	-	approx. 1.0 x 0.7	-	0.22 x 0.08	1.02-1.22
Ovary, mm	-	0.7 x 0.54	-	1.16-2.03 x	?
	-	-	-	1.03-1.16	1.11-1.73 x
Eggs, μ m	-	26-29 x 16-21	-	0.94-1.14 x	0.86-1.14
	-	-	34 x 20	0.94-0.96	0.81-1.08 x
	-	-	-	25-32 x 17-19	0.81-1.02
	-	-	-	-	28-38 x 17-21

The wide, terminal *excretory pore* leads into a Y-shaped excretory vesicle, with dorsal and ventral arms. The basal region is so short that the vesicle appears almost V-shaped. In the forebody the arms run laterally and unite dorsally to the ventral sucker.

The *testes* lie close to the ventral sucker, in tandem and just anteriorly to the middle of the body. The seminal vesicle is fairly narrow, being a convoluted tube lying dorsally to the ventral sucker. It passes into a sinuous pars prostatica, which is invested with a deep layer of gland-cells. The *sinus-sac* is small, but relatively well developed and surrounds the base of the genital atrium. Just within the wall of the sinus-sac the male and female ducts unite, and the narrow hermaphroditic duct passes through the middle of the conical sinus-organ, which lies within the genital atrium. The sinus-organ measures 0.08–0.14 mm × 0.05–0.08 mm. The genital pore occurs mid-ventrally, just posteriorly to the oral sucker.

The *ovary* is smaller than the testes and lies close behind them. The oviduct leaves the ovary anteriorly and Mehlis' gland is situated anteriorly (or in contracted specimens antero-laterally) to the ovary. Laurer's canal opens dorsally at the level of the posterior margin of the ovary. The *uterus*, which forms a uterine seminal receptacle proximally, occupies the bulk of the hindbody, with individual loops reaching into the forebody. The metraterm extends from the ventral sucker to the sinus-sac, and is surrounded by gland-cells. A fairly large 'vitelline reservoir' lies ventrally to Mehlis' gland: this is probably the reduced half of the usual two-sided *vitellarium*, as suggested by Robinson (1934). The remainder of the vitellarium is a ramifying tubular system, occupying much of the dorsal region of the worm's forebody and feeding a single duct passing into Mehlis' gland.

DISCUSSION. This worm appears to be virtually identical to *A. nigroflavum*. The only significant difference between these two species seems to be the nature of the body-surface at the posterior extremity. Although some doubt must be expressed as to the importance of this feature, it has been described by both Robinson and Thulin and has not been reported in specimens described under the appellation *A. nigroflavum* or its synonyms.

Robinson (1934) states that in this species one half of the vitellarium is reduced to a small single follicle lying ventrally to Mehlis' gland, whilst the bulk of the vitellarium, situated in the forebody of the worm, represents the other half of the normally more symmetrical two-sided system. It is difficult to be absolutely certain, from the specimens of this species which we have available, whether Robinson has interpreted this system correctly; but it does not appear to differ from that of *A. nigroflavum*. In a flattened specimen of *A. petasiporum*, however, this 'one-sided' asymmetrical system can be plainly seen (Fig. 8), and it seems almost certain that this is a characteristic not only of the genus, but also of the sub-family.

The structures discussed above, which were used by Robinson to distinguish this species, have been used by Skrjabin (1959) to erect a new genus *Guschanskiana*. He also distinguishes this genus as having a sinus-sac. From the descriptions given above and from the literature, it would appear that the presence of a sinus-sac is a feature common to all species of *Accacladocoelium*. We consider, therefore, in view

of this and in the light of the results discussed above, that there is no valid reason for maintaining *Guschanskiana* as a distinct genus.

Accacladocoelium macrocotyle (Diesing, 1858) Robinson, 1934
(Fig. 7)

Distoma sp. of Bellingham, 1844.

Distomum macrocotyle Diesing, 1858.

Podocotyle macrocotyle (Diesing) Stossich, 1898.

Accacoelium macrocotyle (Diesing) Lühe, 1901.

TYPE-HOST AND LOCALITY. *Mola mola*, Ireland.

RECORDS.

(i) Material studied.

Mola mola [intestine] Skagerrak, Sweden (58°N, 11°E) (Dec. 1929). Natural History Museum of Gothenburg Reg. No. 29-5153.

Mola mola [intestine] Aberdeen, Scotland. BM(NH) Reg. No. 1966.9.6.54.

(ii) From the literature.

Mola mola [intestine] Ireland (July, 1839). Bellingham (1844 : 429 ; as *Distoma* sp.).

Mola mola [intestine] Kattegat at Varberg, Sweden. (Nov.) Olsson (1868 : 24).

Mola mola [intestine] Atlantic WSW of Great Britain (48°N, 19°W) (Sept. 1886). Guiart (1938 : 40).

PREVIOUS DESCRIPTIONS. Monticelli (1893) ; Linton (1940) ; Timon-David & Musso (1971).

DESCRIPTION. Numerous whole specimens, one bisected specimen and one sectioned specimen were available for study. The measurements are summarized in Table 5.

The body-surface may be partly rugate, but bears no plications or spines. The *oral sucker* is globular, with a fairly long anterior process of the small pharynx encroaching into its base. The *pharynx* leads into an elongate and very narrow oesophagus, reaching to the level of the ventral sucker before it passes into the caeca, which have an H-shaped configuration. They communicate with the excretory vesicle close to the posterior end of the worm, forming a uroproct. The *ventral sucker* is longitudinally extended, but does not appear to bear any flanges or similar modifications.

The *excretory pore* is terminal, and leads to a short vesicle, which divides into dorsal and ventral arms that run anteriorly to about the level of the ventral sucker before passing laterally. They unite dorsally to the pharynx.

The two almost globular *testes* lie in tandem near the ventral surface of the worm, closely posterior to the ventral sucker. A convoluted, tubular seminal vesicle lies dorsally to the ventral sucker, and leads into a sinuous and tubular pars prostatica with a well-developed external covering of gland-cells. A very small, but distinct, sinus-organ lies inside a fairly deep genital atrium, and receives both the ejaculatory duct and the metraterm, which join at its base. It appears to be capable of partly or

TABLE 5

 Dimensions of *Accacladocehium macrocotyle* from *Mola mola* as recorded by various authors

Locality	Bellingham, 1844	Monticelli, 1893	Linton, 1898	Linton, 1940	Timon-David & Musso, 1971	Present Study
	Ireland	?	Massachusetts, USA	Massachusetts, USA	Gulf of Marseilles	see text
Length, mm	8.5-10.5	9-18	14	10-13	7.8-10.5	9-18
Max. width, mm	-	-	1.7	1.26-1.54	1.3-1.6	1.48-3.0
Oral sucker, mm	-	-	0.65 dia.	0.50-0.61 x	0.42-0.70 x	0.65-1.08 x
Ventral sucker, mm	-	-	1.4 dia.	0.50-0.56	0.40-0.50	0.69-1.16
Pharynx, mm	-	-	-	1.2-1.33 x	0.82-0.96 x	1.22-2.2 x
Testes, mm	-	-	-	1.0-1.3	1.05-1.19	0.73-1.76
Ovary, mm	-	-	-	0.3 x 0.15	0.19-0.20 x	0.48-0.56 x
Eggs, μ m	-	-	-	-	0.11-0.13	0.15-0.23
					1.09-1.40 x	0.73-1.48 x
					0.94-1.25	0.54-1.35
					0.70-1.12 x	0.46-0.89 x
					0.50-1.08	0.46-0.92
					'à peu près les mêmes dimensions que <i>A. nigroflavum</i> '	30-36 x 19-25
					24 x 18	

completely invaginating itself so that it projects backward into the hermaphroditic duct (Fig. 7b). The *sinus sac* is also small and distinct. The genital pore is mid-ventral, close behind the oral sucker.

The globular *ovary* lies just posteriorly to the testes. Mehlis' gland is directly anterior to the ovary and Laurer's canal opens dorsally at the level of the anterior margin of the ovary. The proximal part of the *uterus* constitutes a uterine seminal receptacle whilst the remainder of the uterus occupies much of the hindbody and contains numerous relatively large eggs. The vitelline duct bifurcates close to Mehlis' gland. Numerous tubular branches of the *vitellarium*, which extend as far as the pharynx, arise from the anterior branch, whilst the other branch passes

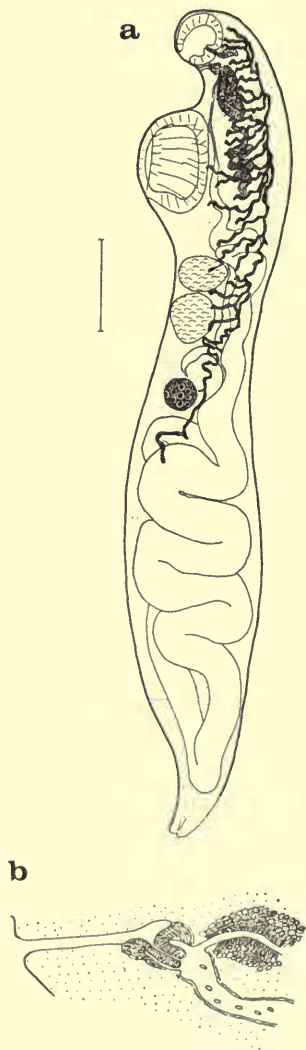


FIG. 7. *Accacladocoelium macrocotyle*: (a) semi-diagrammatic lateral view (gut omitted). Scale - 2 mm. (b) Semi-diagrammatic view of terminal genitalia showing sinus-organ projecting backward into hermaphroditic duct.

posteriorly, being fed by a small number of very short tubules lying in the region just posterior to the ovary. A compact 'vitelline reservoir' was not seen.

DISCUSSION. This species differs from other species of the genus in having a more extensive vitellarium which reaches just posteriorly to the ovary. In this species the reduced half of the vitellarium does not form a saccular reservoir, but is represented by a few very short tubules. This is similar to the condition in *Tetrochetus raynerii* as described by Looss (1912) and below.

Accacladocoelium petasiporum Odhner, 1928

(Fig. 8)

Distoma calyptrocotyle Monticelli of Odhner, 1911.

TYPE-HOST AND LOCALITY. *Mola mola*, Mediterranean Sea.

RECORDS.

(i) Material studied.

Mola mola [intestine] Kattegat at Gothenburg, Sweden. Material lent by J. Thulin.

(ii) From the literature.

Mola mola [intestine] Kattegat at Gothenburg, Sweden (Nov. 1971). Thulin (1973: 83).

DESCRIPTION. This description is based upon two well-flattened and whole-mounted specimens, one of which has been cut in two. Description from flattened specimens is not to be recommended; but, as it appears that this species has never been adequately described, it seems warranted in this case. The morphology of the specimens has, no doubt, been altered by the flattening process, and this should be taken into account in considering this description. See Table 6 for the dimensions of this worm.

TABLE 6

Dimensions of *Accacladocoelium petasiporum* from *Mola mola*,
Kattegat, Sweden

	Thulin, 1973	Present Study
Length, mm	10.4	8.0-10.2
Max. width, mm	1.2	0.94-1.2
Oral sucker, mm	-	0.45-0.47 × 0.45-0.52
Ventral sucker, mm	-	0.70-0.84 × 0.89-1.04
Pharynx, mm	-	0.10-0.12 × 0.12-0.16
Testes, mm	-	0.62-0.76 × 0.76-1.0
Ovary, mm	-	0.40-0.43 × 0.41-0.54
Eggs, μ m	35 × 18	32-39 × 19-21

The body-surface of this elongate worm is smooth. The *oral sucker* is rounded and ventro-terminal. The *ventral sucker* is larger than the oral sucker and is situated on a distinct, but short, peduncle in the anterior half of the body. This sucker is

clearly modified in that it possesses wing-like lateral muscular extensions or flanges (Fig. 8).

The morphology of much of the alimentary system could not be made out in these preparations; but the *pharynx* with an anterior extension into the base of the oral sucker and the caeca with the anterior arms, both so characteristic of the accacoliines, are present. A uroproct may be present, as the caeca extend close to the excretory pore. Similarly, much of the excretory system could not be seen in these preparations. All that can be distinguished is that the excretory pore is terminal, and that the stem of the Y-shaped vesicle is short.

The large oval *testes* are in tandem in the anterior half of the hindbody. The seminal vesicle is narrow, convoluted and very long, reaching back in one specimen to the anterior testis, and nearly so in the other (Fig. 8). The tubular pars prostatica is enveloped by a wide region of gland-cells and extends forward sinuously from about the middle of the forebody to the junction with the hermaphroditic duct. Although the details of the musculature of the *sinus-sac* and sinus-organ are not visible, a definite, if short, sinus-organ is visible surrounding the distal part of the hermaphroditic duct. The proximal region of this duct is dilated in one specimen, and appears to contain an accumulation of sperm. The sinus-organ is present within a small genital atrium, and the genital pore occurs mid-ventrally, close to the posterior margin of the oral sucker.

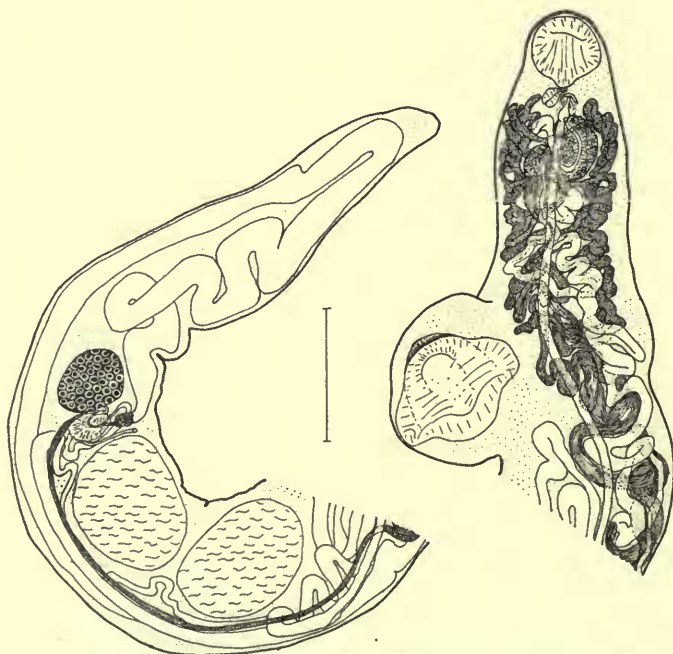


FIG. 8. *Accacladocoelium petasiporum*: flattened specimen (gut omitted).
Scale - 1 mm.

The globular *ovary* lies posteriorly to the testes, and Mehlis' gland is present between the ovary and the testes. Laurer's canal is present, and can be seen in one specimen to open to the exterior at about the level of the hind margin of the posterior testis. The *uterus* leads posteriorly from the ovary almost to the posterior extremity of the worm, where it turns and runs forward directly past the gonads. It then follows a convoluted course up into the anterior region of the forebody, returns to the pre-testicular region of the hindbody and finally passes anteriorly again as a long, narrow and relatively straight metraterm (Fig. 8), uniting with the pars prostatica near the base of the sinus-organ. The eggs are rather larger than occur in most species of this genus. The *vitellarium* consists of a large ramifying system of tubules lying in the forebody, and which are connected by a single, long collecting duct to Mehlis' gland. The other half of the vitellarium is reduced to a small oval sac (? reservoir), which measures 0.1×0.08 mm and is connected to Mehlis' gland by a short duct.

DISCUSSION. This species was named by Odhner (1928) for certain specimens which he found amongst Monticelli's and Stossich's material from the Mediterranean and labelled *Distoma macrocotyle*. Earlier Odhner (1911), because of the presence of a 'collar' on the ventral sucker, had considered these specimens to be the adults of *Distoma calyptrocotyle* (now *Odhnerium calyptrocotyle*), the immature forms of which had been described by Monticelli (1893) from *Beroe ovata*. In 1928, however, Odhner corrected this error, noting that the 'collar' of the ventral sucker is smaller than that in *D. calyptrocotyle*. Nevertheless, *A. petasiporum* is not clearly recognizable from Odhner's comments. Dollfus (1935), however, managed to obtain some of Odhner's specimens and figured the external details of a specimen of about 3 mm in length. He also pointed out that this species possesses a copulatory organ (sinus-organ), which is lacking in *Odhnerium*. Our best clues as to the morphology of *A. petasiporum* come from Dollfus' key which states: 'L'acetabulum présente des expansions musculaires. Organe copulateur présent. Branches de l'intestin brièvement ramifiées. Vitellogénés plus ou moins rassemblés en petits cordons sinueux entre le pédoncule acétabulaire et le pore génital.' He states that he hoped to publish a comparative study of this species and *O. calyptrocotyle*, but this does not yet appear to have been carried out.

RHYNCHOPHARYNX Odhner, 1928

DIAGNOSTIC FEATURES. Forebody papillate. Ventral sucker pedunculate. Pharynx consisting of two muscular bulbs and an extended anterior snout, which may extend through the oral sucker. Oral sucker possesses posterior glandular extension which envelops the snout. Glandular oesophageal bulb present immediately posterior to pharynx. Oesophagus reaches to ventral sucker. Large glandular organ of unknown function at base of peduncle. Pars prostatica long. Sinus-sac surrounds base of genital atrium. Sinus-organ small. Vitellarium extends from anterior region of ventral sucker to ovary. Parasitic in intestine of marine teleosts (*Mola*).

TYPE-SPECIES. *Rhynchopharynx paradoxa* Odhner, 1928 (by original designation).

Rhynchopharynx paradoxa Odhner, 1928

(Figs 9 and 10)

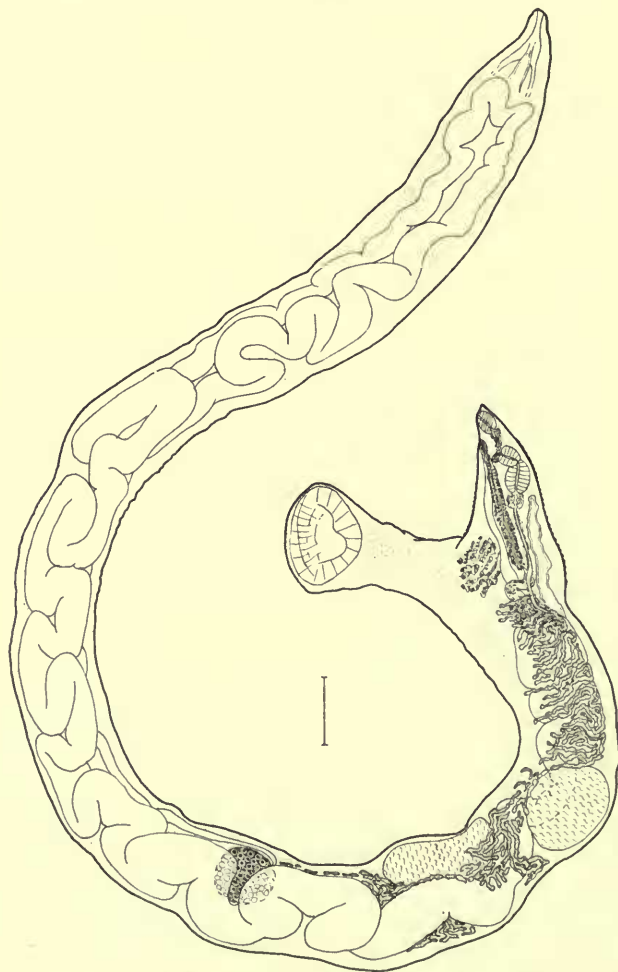
TYPE-HOST AND LOCALITY. *Mola mola*, Trieste.

RECORDS.

(i) Material studied.

Mola mola [intestine] Väderöarna Islands, Sweden (59°N, 11°E) (Sept. 1941).

Natural History Museum of Gothenburg Reg. No. 41-7819.

Mola mola [intestine] Havstenssund, Sweden (59°N, 11°E) (Aug. 1941). Natural History Museum of Gothenburg Reg. No. 41-7805.(?) *Mola mola* [intestine] Locality unknown. Donor: Zool. Museum, Amsterdam. BM(NH) Reg. No. 1946.12.20.42.FIG. 9. *Rhynchopharynx paradoxa*: lateral view (most of gut omitted).

Scale - 1 mm.

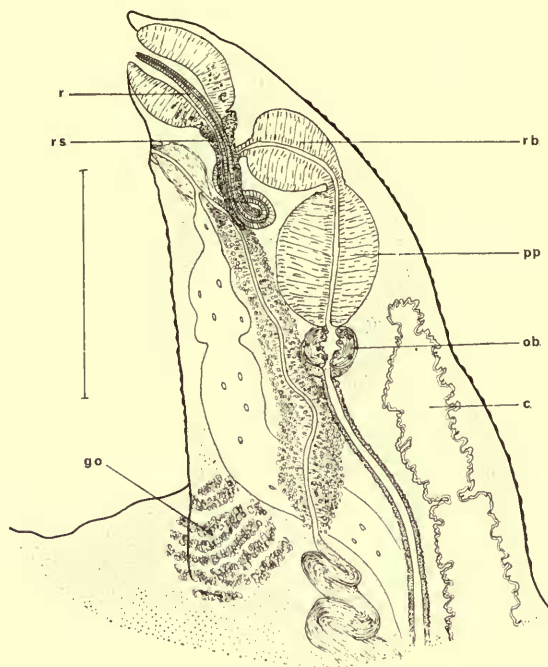


FIG. 10. *Rhynchopharynx paradoxa*: detail of forebody. Scale = 1 mm. c., caecum; g.o., glandular organ; o.b., oesophageal bulb; p.p., pharynx proper; r., 'Rüssel'; r.b. 'Rüsselblase'; r.s., 'Rüsselscheide'.

(ii) From the literature.

None.

PREVIOUS DESCRIPTIONS. Odhner (1928); Yamaguti (1934).

DESCRIPTION. These worms (four whole-mounts and one sectioned) are very elongate. The *ventral sucker* is situated close to the anterior end of the body on an extensible peduncle, which may reach 3 mm in length (Fig. 9). The body surface may be rugate, and bears papillae on the forebody, but lacks spines or plications. The aperture of the ventral sucker appears to be extended antero-posteriorly. The *oral sucker* is roughly globular with a glandular posterior extension in the form of a tube: the glands being enclosed in a thin muscular sheath, and similar gland-cells may be seen in the musculature of the oral sucker (Fig. 10). The glandular tube surrounds the anterior process, the 'Rüssel' or snout, of the *pharynx* and is known as the 'Rüsselscheide' or snout-sheath. This snout portion of the pharynx is muscular and elongate, up to about 1.5 mm in length by 0.03 mm at its distal end and 0.09 mm near its proximal end, and it may extend as an elongate papilla into the lumen of the oral sucker. It is recurved within the anterior region of the body and widens out to form an anterior, muscular bulb, the 'Rüsselblase' or snout-bladder, of the pharynx, which measures 0.28–0.45 × 0.42–0.48 mm. A short, narrow,

TABLE 7

Dimensions of *Rhynchopharynx paradoxa* from *Mola mola* as recorded by various authors

	Odhner, 1928	Yamaguti, 1934	Present Study
Locality	Trieste	Pacific Ocean	see text
Length, mm	20-31.5	36	20-35
Max. width, mm	1.5-2.0	-	1.7-2.5
Oral sucker, mm	0.48-0.57 × 0.34-0.45	0.37 × 0.32	0.38-0.45 × 0.46-0.52
Ventral sucker, mm	1.25-1.4	1.26 × 1.0	1.04-1.48 × 1.10-1.48
Pharynx, mm	0.50-0.65	0.37	0.46-0.56 × 0.56-0.78
Testes, mm	-	1.57 × 0.77	1.34-2.05 × 0.72-1.62
Ovary, mm	-	0.95 × 0.74	1.17-1.32 × 1.19-1.32
Eggs, μ m	27-30 × 19	29-32 × 18-21	32-36 × 21-25

muscular tube connects the latter region to a muscular posterior bulb, the pharynx-proper, the measurements of which are given in Table 7. This leads into a small, globular oesophageal bulb, which is a complex mixture of muscular and glandular tissue of about 0.26 mm in diameter (Fig. 10). This in turn leads into a long and very narrow (1.5 × 0.03 mm) oesophagus, which is surrounded by gland-cells. The oesophagus reaches to a level just posteriorly to the peduncle of the ventral sucker, where it bifurcates to form two gut-caeca which have blind anteriorly-directed branches, in addition to posteriorly-directed branches that fuse terminally with the excretory vesicle to form a uroproct.

There is a pair of large glandular organs at the base of the peduncle of the ventral sucker, the function of which is not known. Each consists of numerous, tightly packed gland-cells, arranged in irregular and branching lamina, and which stain darker than the prostatic cells with H. and E.

The *excretory pore* is terminal and leads into a Y-shaped excretory vesicle with ventral and dorsal arms. The hindbody is so packed with eggs that, even in serial sections, it is not possible to trace the course of these arms. In the forebody, however, they can be seen to be muscular and tubular, and pass laterally at the level of the pars prostatica, joining dorsally to the pharyngeal complex.

The very large, oval or irregularly-oval *testes* appear in dorso-ventral view to be in tandem, but the anterior testis lies nearer to the dorsal surface than the posterior testis. They occur in the anterior part of the hindbody. The seminal vesicle is a relatively narrow, convoluted tube lying at about the level of the base of the peduncle of the ventral sucker. It passes forward to join a long, gently undulating pars prostatica which is surrounded by numerous closely-packed gland-cells. The pars prostatica extends forward to the base of a relatively small oval *sinus-sac*, which has a very diffuse wall and measures 0.26 mm in length. There is a short ejaculatory duct within the sinus-sac, which joins with the metraterm to form an hermaphroditic duct. The latter runs through the sinus-sac and opens at the apex of a short sinus-organ, measuring about 0.08 mm in serial section. It lies within a shallow genital atrium, which opens to the surface through the genital pore situated mid-ventrally at the level of the posterior margin of the oral sucker.

The sub-globular *ovary* is situated posteriorly to the testes, being separated from the posterior testis by coils of the uterus. Mehlis' gland lies nearly contiguous with the anterior margin of the ovary, and Laurer's canal can be seen to pass anteriorly and dorsally to the ovary. The great extent of the uterus tends to hamper sectioning, and thus the remainder of Laurer's canal and the pore were not observed. The first coils of the *uterus* form a uterine seminal receptacle situated anteriorly to Mehlis' gland. The uterus then passes posteriorly, almost to the posterior extremity, before looping forward and filling much of the hindbody. It passes into the forebody, and, in the form of a wide tube, reaches the base of the sinus-sac. It narrows as it passes through the wall of the sinus-sac, after which the short metraterm unites with the ejaculatory duct to form the hermaphroditic duct. Ventrally to Mehlis' gland there lies a fairly large, subglobular 'vitelline reservoir' of about 0.1 mm in diameter. It is connected by a short duct to the oviduct. The remainder of the *vitellarium* consists of numerous, complex, ramifying tubules, which reach from the level of the peduncle of the ventral sucker to the anterior margin of the ovary, and which feed a single collecting duct.

DISCUSSION. Although *Rhynchopharynx* has been recorded from the Mediterranean Sea and from off Japan, it has not, hitherto, been recorded from the north-east Atlantic. *Rhynchopharynx* is a monospecific genus, which is unmistakable, owing to the complicated and unusual modifications of the pharynx.

ODHNERIUM Yamaguti, 1934

Mneiodhneria Dollfus, 1935.

Caballeriana Skrjabin & Guschanskaja, 1959.

DIAGNOSTIC FEATURES. Body-surface smooth, but with muscular sucker-like pads on antero-dorsal surface. Flange-like muscular extensions on ventral sucker; ventral sucker pedunculate. Oesophagus reaches to ventral sucker. Pars prostatica reaches half-way back to ventral sucker. Diffuse muscular region surrounds distal part of metraterm and genital atrium (may be vestige of sinus-sac). Male duct enters genital atrium from side through small papilla. Vitellarium tubular, extending from pharynx to ovary. Parasitic in intestine of marine teleosts (*Mola*).

TYPE-SPECIES. *Odhnerium calyptrocotyle* (Monticelli, 1893) (by original designation).

Odhnerium calyptrocotyle (Monticelli, 1893) Yamaguti, 1934

(Figs 11 and 12)

Distoma nigroflavum Rudolphi of Olsson, 1868.

Distoma calyptrocotyle Monticelli, 1893.

Orophocotyle calyptrocotyle (Montic.) Looss, 1902.

Accacoelium calyptrocotyle (Montic.) Stiles & Hassall, 1908.

Mneiodhneria calyptrocotyle (Montic.) Dollfus, 1935.

Distoma foliatum Linton, 1898.

Orophocotyle foliatum (Linton) Looss, 1902.

Accacoelium foliatum (Linton) Stafford, 1904.

Mneiोधneria foliata (Linton) Dollfus, 1935.

Caballeriana lagodovsky Skrjabin & Guschanskaja, 1959.

TYPE-HOST AND LOCALITY. *Beroe ovata*, Naples, Italy.

RECORDS.

(i) Material studied.

Mola mola [intestine] Skagerrak, Sweden (58°N, 11°E) (Dec. 1929). Natural History Museum of Gothenburg Reg. No. 29-5153.

Mola mola [intestine] Hunnebostrand, Skagerrak, Sweden (58°N, 11°E). Natural History Museum of Gothenburg Reg. No. 36-4970.

Mola mola [intestine] Havstenssund, Skagerrak, Sweden (59°N, 11°E) (Aug. 1941). Natural History Museum of Gothenburg Reg. No. 41-7805.

Mola mola [intestine] Toras Ungar Islands (between Bonden and Hallo Islands), Skagerrak, Sweden (58°N, 11°E) (Sept. 1941). Natural History Museum of Gothenburg Reg. No. 41-7813.

Mola mola [intestine] Rockall, North East Atlantic. BM(NH) Reg. No. 1964.7.16.21-35.

Mola mola [?] Locality unknown. Donor: Zool. Mus. Amsterdam. BM(NH) Reg. No. 1946.12.20.27-41.

(ii) From the literature.

Mola mola [intestine] Varberg, Kattegat, Sweden (Nov.). Olsson (1868: 25; as *Distoma nigroflavum*).

Mola mola [intestine] Atlantic SW of Ireland (48°N, 09°W) (July 1921); Roscoff, English Channel (Aug. 1921); South of Belle Isle, Bay of Biscay (Aug. 1922). Dollfus (1935: 209 footnote).

Mola mola [intestine] Atlantic WSW of Great Britain (48°N, 19°W) (Sept. 1886). Guiart (1938: 38; as *Mneiोधneria foliata*).

PREVIOUS DESCRIPTIONS. Monticelli (1893); Linton (1898, 1940); Yamaguti (1934); Lloyd (1938); Timon-David & Musso (1971).

LIFE-HISTORY. The life-history is not completely known; but this species was originally described from the ctenophore *Beroe ovata*, presumably as a metacercaria.

DESCRIPTION. Numerous whole-mounts and one serially sectioned specimen of these elongate worms have been studied. See Table 8 for the dimensions of these worms. The body-surface may be smooth or rugate, depending on contraction. A peculiar feature is the presence of a series of sucker-like muscular pads on the antero-dorsal region of the body-surface (Figs 11 and 12). The most anterior pads are the largest, and they decrease in size posteriorly, reaching about half-way down the fore-body. The *ventral sucker* is very large and protrudes from the ventral surface of the body, sometimes apparently on a short peduncle. Two muscular flanges arise from the anterior margin and pass down each side of this sucker (Figs 11 and 12). These flanges are fused with the sucker dorsally and extend about three-quarters of the sucker-length.

The *pharynx* extends slightly into the base of the *oral sucker*. It is muscular and longer than wide, and leads, via a short muscular extension, into an elongate narrow

TABLE 8
Dimensions of *Odhnernium calyptrocotyle* as recorded by various authors

Name used	Olsson, 1868	Monticelli, 1893	Linton, 1898	Yamaguti, 1934	Lloyd, 1938	Linton, 1940	Timon-David & Musso, 1971	Present Study
Host	<i>Distoma nigroflavum</i>	<i>Distoma calyptrocotyle</i>	<i>Distoma foliatum</i>	<i>Odhnernium calyptrocotyle</i>	<i>Odhnernium calyptrocotyle</i>	<i>Orophocotyle foliata</i>	<i>Mneiodhneria calyptrocotyle</i>	<i>Odhnernium calyptrocotyle</i>
Locality	Sweden	Trieste	Mass., USA	Japan	Vancouver Is.	Mass., USA	Gulf of Marseilles	<i>Mola mola</i> see text
Length, mm	18-25	2.5-3.5 (imm.)	12	8.95	-	14-15	9-20	7.5-18
Max. width, mm	1.5	-	1.28	0.89	-	0.77-1.12	0.06-0.9	0.58-1.35
Oral sucker, mm	-	-	0.82 x 0.65	0.84 x 0.6	-	0.52-0.72 x 0.21-0.74	0.57-0.83 x 0.48-0.60	0.32-0.60 x 0.36-0.89
Ventral sucker, mm	-	-	1.9 dia.	1.5 long	-	1.33-1.4 x 0.70-1.5	0.72-1.09 x 1.12-1.70	1.30-2.02 x 0.60-1.24
Pharynx, mm	-	-	0.48 long	-	-	0.28-0.44 x 0.15-0.23	0.19-0.28 x 0.28-0.41	0.35-0.45 x 0.15-0.26
Testes, mm	-	-	0.68-1.02 long	0.60-0.80 x	-	-	0.82-1.38 x	0.46-1.35 x
Ovary, mm	-	-	0.43-0.53 dia.	0.52-0.57 0.47 x 0.69	-	-	0.50-0.79 0.49-0.69 x	0.23-0.76 0.30-0.74 x
Eggs, μ m	-	-	32 x 22	34-39 x 21-23	34 x 20	30-33 x 18-21	0.42-0.60 30-35 x 15-20	0.17-0.54 32-40 x 18-27

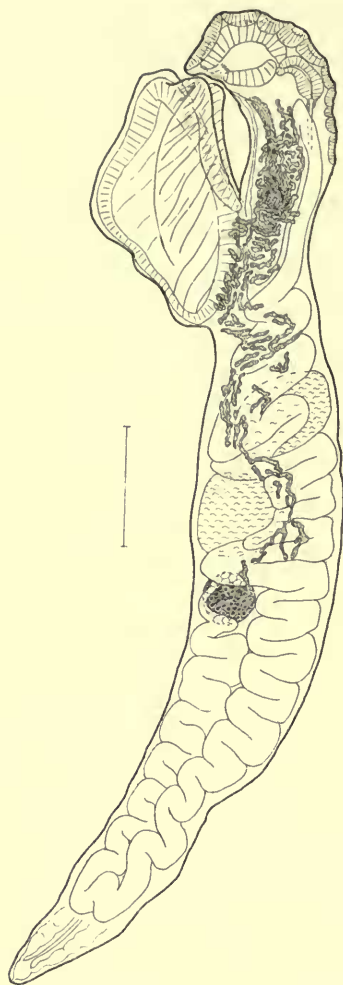


FIG. 11. *Odhnerium calyptrocotyle*: lateral view (gut omitted). Scale — 1 mm.

oesophagus, which reaches to the level of the base of the ventral sucker. It divides into two caeca, which extend anteriorly to the level of the pharynx and posteriorly almost to the posterior extremity, where they unite with the excretory vesicle via narrow ducts to form a uoproct.

The *excretory pore* is terminal and leads into a fairly capacious excretory vesicle. The uterus is so greatly developed in the hindbody that the course of the arms of the excretory vesicle have not been traced, but a convoluted duct can be seen lying dorsally to the pharynx.

The *testes* lie in the anterior half of the hindbody, with the anterior testis lying close to the dorsal surface and the posterior testis, which is separated from it by a few coils of the uterus, lying near the ventral surface. The seminal vesicle is a convoluted tubular structure, lying at about the level of the ventral sucker, or slightly further

forward. It leads into a tubular sinuous pars prostatica, which is lined with cells and surrounded by a thick covering of gland-cells. Although the pars prostatica is fairly long and tubular, it is relatively short when compared with that of most other accacoeiines. The *sinus-sac*, if it may be so termed, is modified to form a narrow, fairly weakly-developed, muscular sheath which surrounds the genital atrium and the distal part of the metraterm. The male duct passes through the dorsal wall of this structure and opens at the base of the genital atrium, often through a very small papilla (Fig. 12). There is no hermaphroditic duct or sinus-organ. It may, however, be possible that what we term the genital atrium is in fact an hermaphroditic duct. If it is a genital atrium, however, the male papilla may be a derivation of the sinus-organ.

The *ovary* lies directly posteriorly to the hind testis, with few coils of the uterus separating them. A large Mehlis' gland lies immediately anterior to the ovary. Laurer's canal passes over the antero-dorsal surface of the ovary and opens dorsally at about the level of the posterior margin of the ovary. The proximal coils of the *uterus* are distended with spermatozoa, forming a uterine seminal receptacle which reaches as far forward as the anterior margin of the posterior testis. The remainder of the uterus occupies the majority of the hindbody and passes anteriorly to about



FIG. 12. *Odhnerium calyptrocotyle*: longitudinal section of forebody. Scale - 1 mm. c., caecum; e.v., excretory vesicle; m., metraterm; m.p., male papilla; o., oesophagus; p., pharynx; p.p., pars prostatica; s.p., sucker-like muscular pads; s.s., sinus-sac; s.v., seminal vesicle; u., uterus; v., vitellarium.

the level of the pharynx. It contains numerous small eggs which vary considerably in size. The narrow muscular metraterm originates at about the level of the ventral sucker, and passes anteriorly close to the ventral surface of the body and leads directly into the genital atrium. As stated above, it is surrounded distally by a muscular sheath, which appears to be homologous with the sinus-sac of other accacoeiliids. The *vitellarium* consists of numerous, ramifying tubules present on both sides of the body, which extend from the level of the pharynx to the ovary. The reduced left side of the vitelline system forms a 'reservoir' which lies ventral to Mehlis' gland.

DISCUSSION. Odhner (1928), after studying some of Linton's specimens of *Distoma foliatum* from *Mola mola*, considered them to be the mature form of *D. calyptrocotyle*, which up to that time had only been described from the ctenophore *Beroe ovata*. Linton's (1898) description is fairly meagre, but no essential difference between it and *D. calyptrocotyle* has been found. The description of *Odhnerium calyptrocotyle* by Lloyd (1938) from the Pacific coast of the USA was used by Skrjabin & Guschanskaja (1959) to erect a new genus and species, *Caballeriana lagodovsky*. The new genus was separated from *Odhnerium* by having 'ventral sucker pedunculate, without appendages'. Dollfus (1960a), after studying these characters, concluded that there is no basis to them. Briefly, Skrjabin & Guschanskaja's differences can be dismissed thus: (1) the ventral sucker often appears to be surmounted on a short peduncle, but sometimes this is not immediately evident [indeed, when the peduncle is as short as it is in Lloyd's figure, it could easily be reduced to nothing by a small amount of contraction, and Monticelli's immature specimens, as figured by him, could quite conceivably be interpreted as possessing a short peduncle]; and (2) the appendages on the ventral sucker of *O. calyptrocotyle* are clearly shown in Lloyd's fig. 35.

In some respects this genus falls in between Dollfus' (1935) conception of the Accacoeiliinae and the Tetrochetinae, which depends essentially only upon the presence or absence of a sinus-organ. In *Odhnerium*, whilst the sinus-organ is absent, the sinus-sac is present, but in a greatly reduced form. Similarly the pars prostatica is shorter than that generally found in the Accacoeiliinae and longer than that of the Tetrochetinae. As these two subfamilies are morphologically very similar and apparently grade into one another, we consider them to be synonymous.

TETROCHETUS Looss, 1912

Paratetrochetus Hanson, 1955.

DIAGNOSTIC FEATURES. Body surface smooth. Ventral sucker pedunculate. Oesophagus fairly long to long. Diverticula present at intestinal bifurcation. Pars prostatica short, straight, narrow. Sinus-sac and sinus-organ absent. Male and female ducts open together into shallow genital atrium. Vitellarium tubular, in hindbody. Parasitic in intestine of marine teleosts with a diet of coelenterates, ctenophores and chaetognaths as well as in carnivorous marine teleosts.

TYPE-SPECIES. *Tetrochetus raynerii* (Nardo, 1833) (by monotypy).

***Tetrochetus raynerii* (Nardo, 1833*) Looss, 1912, emend.**

(Fig. 13)

Distoma raynerium Nardo, 1833.*Distomum raynerianum* Nardo, 1833 of Diesing, 1850.*Accacoelium raynerianum* (Nardo) Lühe, 1901.*Tetrochetus raynerianus* (Nardo) of Dollfus, 1935, and Fukui & Ogata, 1935.TYPE-HOST AND LOCALITY. *Luvarus imperialis*, Venice, Italy.

RECORDS.

(i) Material studied.

Luvarus imperialis [intestine] Vinnesvåg, near Bergen, Norway (Sept. 1918).

University of Bergen Zoological Museum Reg. No. 43779.

Luvarus imperialis [intestine] Lepsøy, near Bergen, Norway (Aug. 1946). University of Bergen Zoological Museum No. 43780.

(ii) From the literature.

None.

PREVIOUS DESCRIPTIONS. Lühe (1901); Looss (1912).

LIFE-HISTORY. Metacercariae of this genus are known to occur in the siphonophore *Physalia* (Okada, 1932; Dollfus, 1960a) and probably also occur in chaetognaths (Dollfus *et al.*, 1955; Dollfus, 1960a, b). Dollfus (1960a) records one free in the plankton. As *Luvarus* feeds on medusae and similar gelatinous planktonic animals, it appears that *Tetrochetus raynerii* is passed directly from its invertebrate second intermediate host to its final host. Other species of *Tetrochetus*, on the other hand, are found in predatory fishes and probably have a third intermediate stage in their life-history, as they have also been recorded from pelagic fishes.

DESCRIPTION. Nine specimens of this worm were kindly lent to us by Professor A. Brinkmann Jr, of the University of Bergen. Six specimens are flattened whole-mounts, one is an unflattened whole-mount and two are serially sectioned. The dimensions are given in Table 9.

These worms are large and elongate, with a prominent *ventral sucker* on a short peduncle in the anterior quarter of the worm. The body-surface is smooth. The globular *oral sucker* is invariably larger than the ventral sucker and opens subterminally. A narrow anterior extension of the *pharynx* protrudes into the posterior wall of the oral sucker. The pharynx widens posteriorly, and leads into a straight, narrow oesophagus 0.62–2.16 mm in length, which is surrounded by a concentration of gland-cells near its junction with the pharynx. At the intestinal bifurcation a few small diverticula radiate. The overall configuration of the intestine is H-shaped, and a uroproct is present. There are numerous gland-cells scattered in the parenchyma of the forebody.

The stem of the *excretory vesicle* is short, dividing near the uroproct and giving rise to dorsal and ventral arms. Wide convoluted tubules can be seen lying laterally in

* Contrary to Stiles & Hassall's (1908) catalogue we have been unable to find the use of the name *Distoma raynerianum* in Nardo (1827), or (1828). We have emended the specific name, placing it in the genitive case, as Nardo (1875) clearly states that he named the species after Prof. S. A. Renier.

TABLE 9

Dimensions of *Tetrochetus raynerii* from *Luvarus imperialis* as recorded by various authors

	Lühe, 1901	Looss, 1912	Present Study (flattened)	Present Study (unflattened)
Locality	Trieste	Trieste	Norway	Norway
Length, mm	10	11-12	9-15	11.5
Max. width, mm	c. 1.5	1-1.3	1.6-3.5	1.76
Oral sucker, mm	c. 1.2 dia.	1.2-1.3 dia.	1.05-2.03 x 1.05-1.68	0.94 x 0.84
Ventral sucker, mm	c. 1.0 dia.	0.9-1.0 dia.	0.67-1.15 x 0.33-1.08	0.73 x 0.51
Pharynx, mm	-	0.42 (plus ant. ext.) x 0.33	0.61-1.02 x 0.23-0.43	0.61 x 0.34
Testes, mm	-	-	0.52-1.43 x 0.35-1.24	0.56-0.74 x 0.48-0.52
Ovary, mm	-	-	0.41-1.02 x 0.30-0.54	0.52 x 0.48
Eggs, μ m	34 x 17	30-35 x 18	32-34 x 19-23	32 x 19

the forebody, and they are prominent in the area ventral to the pharynx. A transverse tubule is visible dorsally to the oral sucker, and it seems probable that this is the union of the excretory arms (see Looss, 1912); but the complete system in this region has not been traced.

The *testes* are relatively small, subglobular to oval, and lie in the anterior half of the hindbody, obliquely in lateral view, with the anterior testis near to the dorsal surface and the posterior near to the ventral surface. The long, narrow, tubular seminal vesicle reaches almost to the anterior testis. It lies, for most of its length, near to the dorsal surface of the worm; but about half-way along the forebody it passes ventrally and runs into a straight pars prostatica, 0.73-1.35 mm in length. The pars prostatica, which is surrounded by a thin layer of gland-cells, enters the base of a small, narrow, genital atrium. The genital pore is situated ventrally to the oral sucker. There is no sign of a sinus-organ, *sinus-sac* or hermaphroditic duct.

The reniform *ovary* lies posteriorly to the testes, near to the ventral margin of the body. In the concavity of the anterior surface of the ovary lies a globular Mehlis' gland, 0.20-0.35 mm in diameter. Laurer's canal runs in a rather straight course from Mehlis' gland to open dorsally at the level of the ovary. The initial coils of the *uterus* constitute a uterine seminal receptacle. The uterus, which contains numerous small eggs, is rather less extensive than is usually the case in accacoelins. First of all, it passes anteriorly as far as the level of the anterior margin of the ventral sucker. It then turns and runs to a short distance from the posterior extremity, where it turns again and passes anteriorly, gradually becoming wider. Finally, the uterus narrows to form a metraterm at about the level of the intestinal bifurcation. The latter duct is narrow, and runs in a straight course to the base of the genital atrium, which it enters ventrally to the pars prostatica. The *vitellarium* consists of numerous narrow, branching tubules extending from about the level of the ventral

sucker to the ovary. It feeds a single collecting duct. The other side of the vitellarium is reduced to a short blind tubule, which may bear several very short branches.

DISCUSSION. This species is found exclusively in *Luvarus imperialis* [= *Ausonia cuvieri*, = *Proctostegus prototypus*] and has previously been found only in the

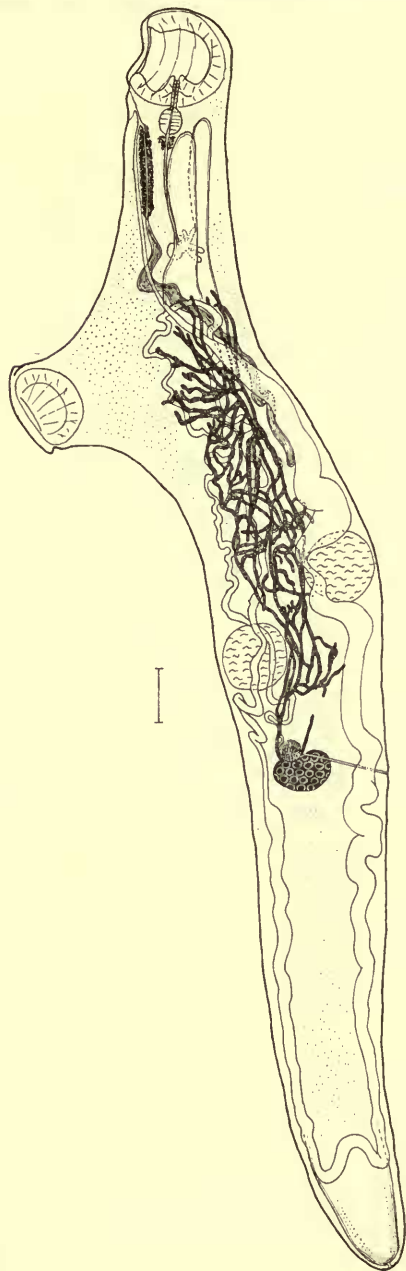


FIG. 13. *Tetrochetus raynerii*: flattened specimen (most of gut omitted). Scale - 1 mm.

Mediterranean basin, i.e. in the Adriatic Sea (Nardo, 1833; Lühe, 1901; Looss, 1912) and in the Tyrrhenian Sea (Parona, 1902). This fish is rather rare, not only in the north-east Atlantic, but throughout its almost world-wide range (Topp, 1973).

Of the other species of *Tetrochetus*, the one most likely to be found in our area in the future is probably *T. coryphaenae* Yamaguti, 1934, which occurs in the dolphin-fish *Coryphaena* elsewhere in the Atlantic Ocean. This species, which has recently been described in detail from the south Atlantic by Gibson (1976), differs from *T. raynerii* in having a ventral sucker distinctly larger than the oral sucker, and in being a considerably smaller and narrower worm.

Subfamily **PARACCACLADIINAE** subfam. nov.

DEFINITION. Accacoeliidae. Body slender. Ventral sucker borne on small peduncle. Body-surface without spines or plications; papillae on outer surface of ventral sucker. Oral sucker with internal ridge. Prepharynx absent. Pharynx protruding into base of oral sucker; otherwise unmodified. Oesophagus short, wide. Caeca with small 'shoulders', but without anterior extensions, terminate blindly near posterior extremity. Testes symmetrical to tandem, in anterior half of hindbody. Seminal vesicle tubular, convoluted; dorsal to ventral sucker and in forebody. Pars prostatica elongate, convoluted. Ejaculatory duct unites with metraterm within sinus-sac. Sinus-sac surrounding base of genital atrium; with diffuse musculature. Sinus-organ short; cylindrical. Hermaphroditic duct within sinus-organ. Genital atrium relatively large; contains sinus-organ. Genital pore mid-ventral in anterior forebody. Ovary globular, post-testicular. Mehlis' gland post-ovarian, linked to posterior region of ovary by oviduct. Laurer's canal with dorsal pore. Uterine seminal receptacle present. Uterus extensive in hindbody. Eggs fairly small; numerous. Vitellarium with branching tubules; symmetrical with two main lateral collecting ducts; in region mainly lateral and posterior to ovary. Excretory vesicle Y-shaped; with arms situated dorsally and ventrally in hindbody and laterally in forebody, uniting dorsally to pharynx. Immature forms in rectum of teleosts with diet of coelenterates, ctenophores and chaetognaths, adults in rectum of carnivorous teleosts (*Coryphaenoides*).

TYPE AND ONLY GENUS. *Paraccacladium* gen. nov.

PARACCACLADIUM gen. nov.

DEFINITION. As subfamily.

TYPE SPECIES. *Paraccacladium jamiesoni* sp. nov.

DISCUSSION. The above detailed definition of the subfamily will serve, for the present time, to define the genus, although both will, no doubt, need to be redefined if further new genera are discovered. *Paraccacladium* appears to be essentially an accacoeliid, but differs in the structure of its alimentary system, the structure of the vitellarium and the position of Mehlis' gland, from all of the genera included in the Accacoeliinae. The accacoeliines have a long, narrow, oesophagus, an H-shaped gut,

a uroproct, a one-sided vitellarium (i.e. with one main collecting duct plus one which is usually rudimentary), and Mehlis' gland lying anteriorly, antero-laterally or antero-dorsally to the ovary. *Paraccacladium* has a short, wide oesophagus, only small caecal 'shoulders', no uroproct, a symmetrical vitellarium with two main collecting ducts, and Mehlis' gland posterior to the ovary (Fig. 1). Its pharynx, however, is typically accacoeliid, as it protrudes into the base of the oral sucker, and the presence of immature forms in teleosts which feed on coelenterates suggests that the metacercariae occur in the same invertebrate groups as the accacoeliines.

Paraccacladium jamiesoni sp. nov.

(Figs 14 and 15a)

TYPE-HOST AND LOCALITY. *Coryphaenoides rupestris*, 55°N, 11°W.

RECORDS.

(i) Material studied.

Coryphaenoides rupestris [rectum] Off west coast of Great Britain :

50°N, 12°W ; depth 965–980 m ; April 1973 (2 specimens).

51°N, 14°W ; depth 920–960 m ; April 1973 (1 specimen).

55°N, 11°W ; depth 800–820 m ; April 1973 (5 specimens).

56°N, 09°W ; depth 780–790 m ; April 1973 (1 specimen).

57°N, 09°W ; depth 560–572 m ; April 1973 (4 specimens).

58°N, 10°W ; depth 780–800 m ; April 1973 (4 specimens).

59°N, 09°W ; depth 720–860 m ; April 1973 (3 specimens).

59°N, 08°W ; depth 570–700 m ; June 1974 (1 specimen).

59°N, 08°W ; depth 880–900 m ; June 1974 (3 specimens).

54°N, 14°W ; depth 1050 m ; June 1974 (7 specimens).

56°N, 17°W ; depth 640 m ; June 1974 (3 specimens).

59°N, 10°W ; depth 1000 m ; June 1974 (2 specimens).

Holotype : BM(NH) Reg. No. 1975.10.31.1.

Paratypes : BM(NH) Reg. No. 1975.10.31.2–18.

(ii) From the literature.

None.

LIFE-HISTORY. Immature forms of this genus have been found in the rectum of *Alepocephalus bairdii*, *Schedophilus medusophagus*, *Centrolophus niger* and *Xenodermichthys copei* (see below), all of which feed upon coelenterates and ctenophores, especially medusae, the presumed second intermediate hosts of accacoeliids. These fishes may act as paratenic hosts, or, more likely, they may be obligatory, particularly as the mature adult has only been found in the carnivorous macrourid *Coryphaenoides rupestris*. It is worth noting that one infested specimen of *Alepocephalus bairdii* was found with its stomach full of the bathypelagic scyphomedusa *Atolla wyvillei*.

DESCRIPTION. Eleven mature specimens were present and all of the remainder were immature, exhibiting varying degrees of immaturity. The dimensions of the main features, including those for *Paraccacladium* sp. (see below), are given in Table 10.

TABLE IO
Dimensions of *Paracaccladium jamiesoni* and *Paracaccladium* sp. immat.

Host	<i>Paracaccladium jamiesoni</i>		<i>Alepocephalus bairdii</i>	<i>Paracaccladium</i> sp. immat.	<i>Schedophilus medusophagus</i>	<i>Xenodermichthys copei</i>	<i>Centrolophus niger</i>
	<i>Coryphaenoides rupestris</i>	<i>Coryphaenoides rupestris</i>					
State of maturity	Mature	Immature	Immature	Immature	Immature	Immature	Immature
Length, mm	3.08-6.4	1.48-3.83	1.34-3.73	1.22	2.9	2.54	2.54
Width at ventral sucker, mm	0.64-0.71	0.37-0.48	0.5-0.64	0.23	0.39	0.32	0.32
Oral sucker, mm	0.38-0.41 x 0.38-0.48	0.22-0.35 x 0.24-0.41	0.23-0.30 x 0.34-0.36	0.16 x 0.15	0.29 x 0.35	0.21 x 0.26	0.21 x 0.26
Ventral sucker, mm	0.35 x	0.2-0.48 x	0.33-0.38 x	0.27 x 0.25	0.32 x 0.39	0.30 x 0.34	0.30 x 0.34
Pharynx, mm	0.64-0.75 0.14-0.27 x	0.31-0.55 0.09-0.12 x	0.36-0.50 0.11-0.15 x	0.074 x 0.053	0.21 x 0.09	0.12 x 0.069	0.12 x 0.069
Oesophagus, mm	0.10-0.16	0.11-0.15	0.12-0.13	?	?	?	?
Anterior testis, mm	0.13-0.24 approx. 0.18-0.36 x	0.08-0.15 approx. 0.062-0.25 x	?	0.13 x 0.10	symmetrical 0.21 x 0.13	0.16 x 0.08	0.16 x 0.08
Posterior testis, mm	0.15-0.19 0.23-0.38 x 0.13-0.28	0.057-0.19 0.098-0.21 x 0.062-0.18	0.10-0.17 0.11-0.20 x 0.11-0.15	0.12 x 0.12	not seen	0.16 x 0.09	0.16 x 0.09
Ovary, mm	0.13-0.33 x 0.13-0.21	0.025-0.18 x 0.025-0.13	0.043-0.13 x 0.043-0.13	0.085 x 0.059	160 x 80 0.3 approx.	0.10 x 0.07	0.10 x 0.07
Sinus-organ, μ m	93-195 x 57-117	88-169 x 57-88	83-170 x 60-85	60 x 49	160 x 80	136 x 56	136 x 56
Pars prostatica	0.27-0.46	0.15-0.27	0.17-0.22	?	0.3 approx.	?	?
Seminal vesicle	0.32-0.54	0.19-0.35	0.10-0.30	?	0.11	0.14	0.14
overall length, mm							
Eggs, μ m	44-53 x 25-28 (in proximal uterus : 39-41 x 18-22)	-	-	-	-	-	-

The worm is long, thin and cylindrical in the case of the mature adults (Fig. 14a), but shorter and stouter in the immature forms (Fig. 15a). The body-surface is smooth, except for numerous dome-shaped papillae, which are present on the outer surface of the ventral sucker, and to a lesser degree on the forebody; these latter papillae are not always readily visible. The *ventral sucker*, which is larger than the oral sucker, lies on a short peduncle just within the anterior third of the body, but further posteriorly in immature forms. The *oral sucker* opens almost terminally, and bears an internal ridge close to the base of the inside wall. This ridge surrounds the dome produced by the extension of the pharynx into the base of the oral sucker. The pyriform *pharynx* leads into a short wide oesophagus, which has a thick cuticular lining. This extends back to about the level of the sinus-organ, where it bifurcates. The two wide caeca, which are lined with a deeply staining epithelium, form small 'shoulders', but not long anteriorly-directed diverticula, and extend posteriorly,

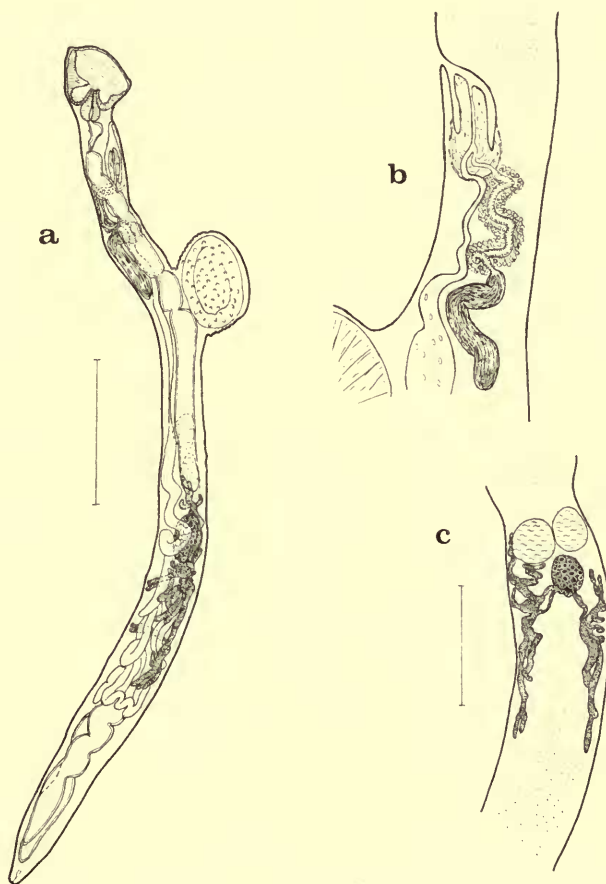


FIG. 14. *Paraccacladium jamiesoni*: (a) lateral view. Scale — 1 mm. (b) Semi-diagrammatic view of terminal genitalia. (c) Ventral view of gonads and vitellarium in an immature specimen. Scale — 0.5 mm.

following a sinuous course, almost to the posterior extremity, where they end blindly.

The *excretory pore* is situated at the posterior extremity and leads into a short convoluted vesicle, which divides to form two anteriorly-directed arms, one ventral and one dorsal. At about the level of the gonads the dorsal duct passes over towards the ventral surface, and then both ducts pass forward ventro-laterally to the level of the pharynx, where they unite dorsally.

The gonads lie in the anterior half of the hindbody, apparently moving further from the ventral sucker as the worm develops, presumably as a result of allometric growth. The smooth, oval *testes* are pre-ovarian, and, in mature specimens, usually lie in tandem, often with the anterior testis lying close to the dorsal surface. Immature specimens show the testes in varying positions from tandem to symmetrical (Fig. 15). The testes are larger than the ovary in immature specimens; but it appears that this species may be protandrous, as in the largest adults the ovary is distinctly larger than the testes. In some very small specimens, although the testes are well developed, no sign of an ovary could be seen. The seminal vesicle is tubular, stout and sinuous, and it extends from about the mid-region of the ventral sucker to a position just anterior to the ventral sucker (Fig. 14b). It leads into a relatively-long tubular pars prostatica, which is surrounded by gland-cells and gently convoluted. The ejaculatory duct unites with the metraterm at the base of the cylindrical sinus-organ to form an hermaphroditic duct, which passes through the sinus-organ and opens terminally. The base of the sinus-organ is enclosed in a diffusely muscular *sinus-sac*, the walls of which are attached to the walls of the genital atrium a little way from its base. The space within the sinus-sac contains numerous muscle-fibres and gland-cells. The external wall of the sinus-organ appears to be a continuation of the wall of the genital atrium, which in turn is similar to that of the external tegument.

The oval *ovary* lies just posteriorly to the testes, near the ventral surface and close to the middle of the body in the largest worms. Immediately behind the ovary is an oval Mehlis' gland, which is rather smaller than the ovary in mature specimens. The oviduct leads into this organ after leaving the ovary posteriorly and receiving Laurer's canal and the common vitelline duct. Laurer's canal runs across the body and opens to the exterior dorsally at the level of the ovary. A uterine seminal receptacle is present and is the sole seminal storage apparatus in the female system. The *uterus* runs posteriorly from the ovary to a point beyond the hindermost end of the vitellarium, but well anteriorly to the posterior extremity of the worm. It then passes anteriorly and winds in the region of the gonads, but then runs forward in a relatively straight or slightly sinuous manner to join the hermaphroditic duct within the sinus-sac in the form of a short metraterm. The uterus contains numerous relatively small eggs, which are noticeably smaller at the proximal extremity of the uterus. The *vitellarium* consists of a symmetrical branching tubular system, possessing two main collecting ducts which pass medially and unite to form a common duct at the level of Mehlis' gland (Fig. 14c). The tubular branches extend laterally between about the level of the posterior testis and a position about half-way between the ovary and the posterior extremity.

***Paraccacladium* sp. (immature)**

(Fig. 15b-e)

RECORDS.

(i) Material studied.

Alepocephalus bairdii [rectum] Off west coast of Great Britain :

51°N, 14°W ; depth 920-960 m ; April 1973 (3 specimens).

55°N, 17°W ; depth 821-850 m ; June 1974 (5 specimens).

57°N, 13°W ; depth 1000-1060 m ; June 1974 (3 specimens).

BM(NH) Reg. No. 1975.10.31.19-21.

Xenodermichthys copei [rectum] Off north-west coast of Scotland :

59°N, 11°W ; depth 970-1025 m ; June 1974 (1 specimen).

BM(NH) Reg. No. 1975.10.31.22.

Schedophilus medusophagus [rectum] Off north-west coast of Scotland :

58°N, 10°W ; depth 780-800 m ; April 1973 (1 specimen).

BM(NH) Reg. No. 1975.10.31.23.

Centrolophus niger [rectum] Off north-west coast of Scotland :

57°N, 13°W ; depth 800-820 m ; June 1974 (1 specimen).

BM(NH) Reg. No. 1975.10.31.24.

(ii) From the literature.

None.

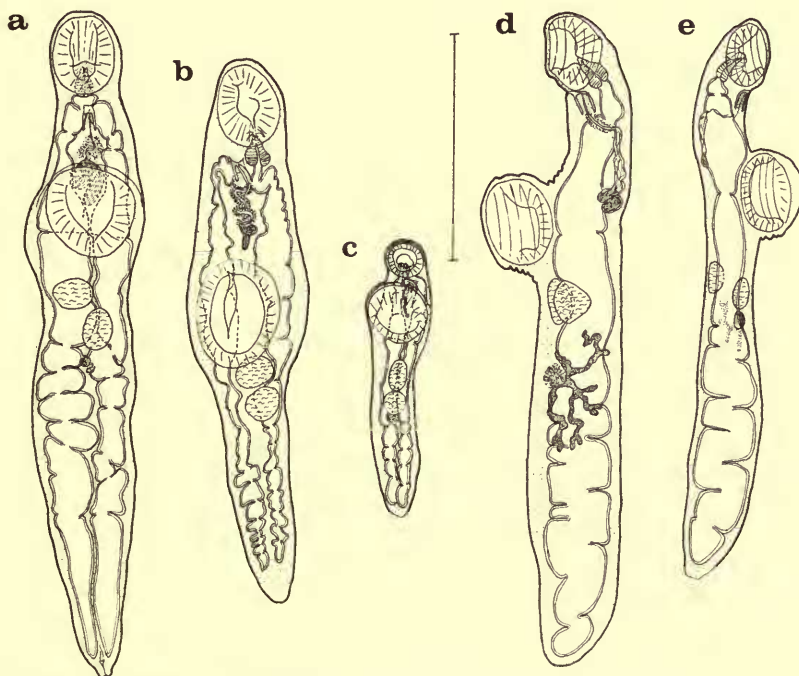


FIG. 15. *Paraccacladium jamiesoni*: (a) immature specimen from *Coryphaenoides rupestris*. *Paraccacladium* sp. immature: (b) from *Alepocephalus bairdii*; (c) from *Schedophilus medusophagus*; (d) from *Xenodermichthys copei*; (e) from *Centrolophus niger*. Scale - 1 mm.

DESCRIPTION. These specimens are morphologically similar to the immature forms of *P. jamiesoni*. Their measurements are given in Table 10, and specimens from each of the four hosts are illustrated in Fig. 15b-e.

DISCUSSION. These immature specimens probably belong to *P. jamiesoni*, as they do not differ significantly from the immature specimens of this species from *Coryphaenoides rupestris*. A complete series from immature to fully mature was found in the latter fish. The sinus-organ is clearly visible in all of the immature specimens, so that they cannot be confused with *Tetrochetus* Looss, 1912, which also appears to utilize teleosts as intermediate hosts (see Gibson, 1976).

Accacladocoelium leontjevae Korotaeva, 1976, appears to belong to this genus, although some important details are omitted from the original description. Korotaeva found it in the intestine of six diverse species of teleost off the south-east coast of New Zealand. It possesses eggs which are considerably smaller than those of *P. jamiesoni*, and apparently also differs in lacking an oesophagus, but this would be a very unusual feature and needs confirmation. We tentatively consider it, as *Paraccacladium leontjevae* (Korotaeva, 1976) n. comb., to represent the second species of this new genus.

The differences between *Paraccacladium* and the accacoeliines are discussed above. It may, however, be worth drawing attention to the similarity between this species and *Sclerodistomoides pacificus* Kamegai, 1971, from the gall-bladder of *Cypselurus pinnatibarbatulus japonicus* from the Pacific coast of Japan. According to Kamegai (1971), however, *Sclerodistomoides* is a much more robust worm and lacks the definite accacoeliid type of pharynx possessed by *Paraccacladium*, and also apparently the presence of dorsal and ventral excretory arms in the hindbody.

HOST-PARASITE LIST*

Order Salmoniformes

- Alepocephalus bairdii* Goode and Beane : *Paraccacladium* sp. (immature).
Xenodermichthys copei (Gill) : *Paraccacladium* sp. (immature).

Order Gadiformes

- Coryphaenoides rupestris* Gunnerus : *Paraccacladium jamiesoni* gen. et sp. nov.

Order Perciformes

- Centrolophus niger* (Gmelin) : *Paraccacladium* sp. (immature).
Luvarus imperialis Rafinesque : *Tetrochetus raynerii* (Nardo).
Schedophilus medusophagus (Cocco) : *Paraccacladium* sp. (immature).

Order Tetraodontiformes

- Mola mola* (L.) : *Accacoelium contortum* (Rud.).
Accacladium serpentulum Odhner.
Accacladocoelium nigroflavum (Rud.).
Accacladocoelium macrocotyle (Dies.).
Accacladocoelium petasiporum Odhner.

* We have consulted Greenwood *et al.* (1966) for the ordinal names in this checklist.

Accacladocoelium alveolatum Robinson.
Rhynchopharynx paradoxa Odhner.
Odhnerium calyptrocotyle (Monticelli).

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